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Mouthparts of the Burgess Shale fossils *Odontogriphus* and *Wiwaxia*: implications for the ancestral molluscan radula

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The Middle Cambrian lophotrochozoans *Odontogriphus omalus* and *Wiwaxia corrugata* have been interpreted as stem-group members of either the Mollusca, the Annelida, or a group containing Mollusca + Annelida. The case for each classification rests on the organisms' unusual mouthparts, whose two to three tooth-rows resemble both the molluscan radula and the jaws of certain annelid worms. Despite their potential significance, these mouthparts have not previously been described in detail. This study examined the feeding apparatuses of over 300 specimens from the 505-million-year-old Burgess Shale, many of which were studied for the first time. Rather than denticulate plates, each tooth row comprises a single axial tooth that is flanked on each side by eight to 16 separate shoehorn-shaped teeth. Tooth rows sat on a grooved basal tongue, and two large lobes flanked the apparatus. New observations—the shape, distribution and articulation of the individual teeth, and the mouthparts' mode of growth—are incompatible with an annelid interpretation, instead supporting a classification in Mollusca. The ancestral molluscan radula is best reconstructed as unipartite with a symmetrical medial tooth, and *Odontogriphus* and *Wiwaxia* as grazing deposit-feeders.

Keywords: Lophotrochozoa; molluscs; radulae; Cambrian explosion; evolution; lagerstätten

1. INTRODUCTION

Although the molluscs represent the second-largest animal phylum and have a rich shelly fossil record, their early evolutionary history remains contentious. The soft-bodied organisms *Odontogriphus omalus* and *Wiwaxia corrugata* from the Middle Cambrian Burgess Shale (Series 3—505 Ma) seem to represent early members of this group [1,2]; if so, they provide our best constraint on the ancestral mollusc. However, it has been suggested that *Wiwaxia* is more closely related to the annelid worms [3–5], and that *Odontogriphus* could have diverged from a lineage ancestral to both the molluscs and the annelids [4,5]. The fossils' mouthparts, which have been interpreted as a radula (the molluscan feeding apparatus) or as an annelid jaw [1,2,5–8], are pivotal to the classification—but have not been described in detail.

The mouthparts of *Wiwaxia* are understood to represent a series of flexible denticulate plates, with either one [1,9] or two [3,6] plates per row (depending on interpretation). They closely resemble the better-understood *Odontogriphus* feeding apparatus. According to Caron *et al.* [2,7], this consists of two (occasionally three) bilaterally symmetrical tooth rows, with the posterior row usually wider than the anterior. The teeth, which have a consistent relative position even when isolated from the body, are held to have been embedded in or on a non-fossilized radular membrane. Caron *et al.* deduce that this membrane sat upon a supporting apparatus or 'tongue'; teeth occupied its dorsal surface and sometimes passed round to the underside, inverting as they did so. Caron *et al.* go on to interpret the mouthparts as bipartite and distichous: that is, comprising just two denticulate teeth in each symmetrical row, with the radular membrane divided along its centre. The posterior genesis of new tooth rows is inferred from the faintness of the third tooth row, where present. It is not clear whether adjacent rows were the same size; nor whether denticle shape varied between rows.

The present study supplements previously examined material with new specimens collected by the Royal Ontario Museum. One hundred and seventy *Odontogriphus* specimens were examined, of which 155 bore mouthparts; 10 further *Odontogriphus* mouthparts lacked accompanying body tissue. Four hundred and seventy-six *Wiwaxia* specimens were examined, 140 with clear mouthparts, and one isolated *Wiwaxia* apparatus was identified. Backscatter electron micrographs were acquired under environmental pressure [10], complementing traditional light microscopy and digital interference of images obtained under plane-polarized and cross-polarized light [11]. This high-resolution imaging allows a fundamentally new reconstruction of the mouthparts, invalidating their interpretation as an annelid jaw and instead revealing striking similarities with the radula—bringing a new perspective to the origin of this defining molluscan synapomorphy.

2. OBSERVATIONS

(a) *Composition*

The mouthparts are primarily preserved as a non-mineralized film of carbon silhouetted by trace amounts of Ca and P (figure 1). The regions corresponding to the tooth rows are depleted in Si and show raised concentrations

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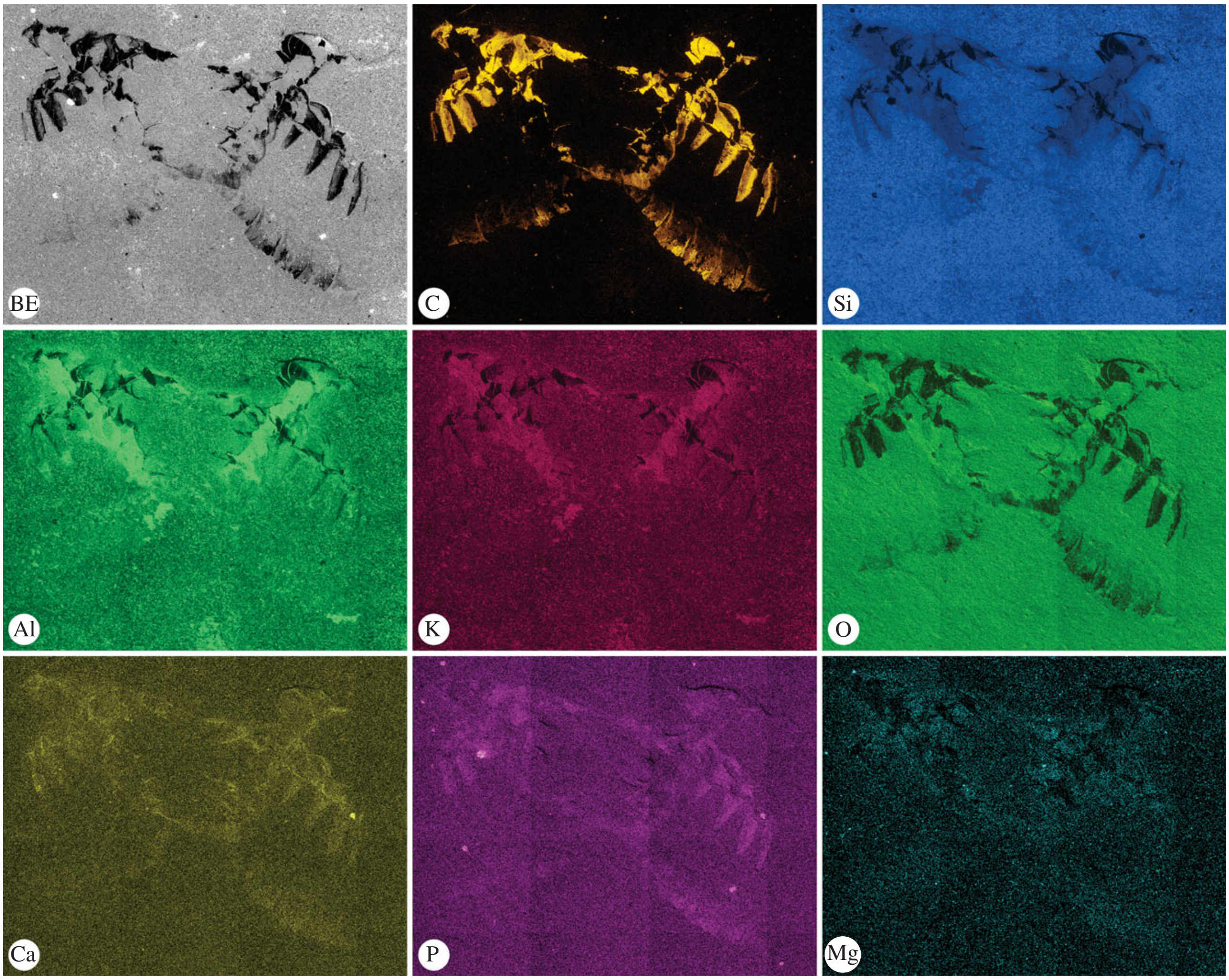

Figure 1. Elemental distribution in the mouthparts of *Odontogriphus omalus*. Royal Ontario Museum (ROM) 57715. BE, backscatter electron image; others, EDS images, brighter areas denote relatively higher elemental abundance. Panel width: 5 mm.

of Al and K: an elemental signature that is commonly associated with voids [12,13]. Along with the thickness of the carbon film, this suggests that the teeth were robust enough to resist compaction—accounting for their heightened relief and their tendency to interrupt the plane of splitting.

(b) *Teeth*

Each of the mouthparts' 'denticulate plates' actually comprises an array of individual articulating teeth (figure 2). Except for a bilaterally symmetrical central tooth in each row, teeth within the same taxon have a consistent shape. Each tooth is shoehorn-shaped, tapering from a pointed root to a broad, flattened scoop. The root sits at the front of each tooth, pointing towards the apex of the chevron (figure 2*b*). The scoops lie either parallel or sub-perpendicular to the bedding plane (figure 2*a*,*b*), indicating that they originally sat at an oblique angle to the tongue. Marginal thickenings (figure 2*b*,*c*) emphasize the slight transverse curvature of each tooth. The ratio of scoop width to root length is around 1 : 1 in *Odontogriphus* but closer to 2 : 1 in *Wiwaxia*.

(c) *Tooth row disposition*

All the examined *Odontogriphus* and *Wiwaxia* specimens bear two tooth rows; some possess a third. This additional posterior row resembles the others, although it is often fainter: probably reflecting its weaker carbonization, its preservation at a different level within the rock, or a combination thereof (figure 3*a*). The total number of tooth rows (two or three) is unrelated to size (binary logistic regression against log(*apparatus width*): adjusted $R^2 = 0.004$, $p = 0.28$, $n = 44$). In *Odontogriphus* the rows are separated by 1.7 ± 0.7 times the width of the widest tooth ($n = 18$), whereas in *Wiwaxia*, tooth rows are immediately adjacent (separation $= 0.18 \pm 0.16$ times maximum tooth width, $n = 14$).

In each *Odontogriphus* tooth row (figures 2 and 3), the central tooth is flanked by nine to 11 medial teeth—of which the abaxial six or seven are substantially larger—and sometimes a further one or two diminutive lateral teeth (figure 2*b*,*c*). When the mouthparts are in their resting position, teeth form anteriad-directed chevrons with a basal angle of $34 \pm 6^\circ$ (irrespective of specimen size; $n = 40$). In their active position, where chevrons have passed around the end of the supporting apparatus and onto its dorsal surface (figure 2*c*), their angle is steeper ($53 \pm 6^\circ$, $n = 8$; two-tailed *t*-test $p < 10^{-4}$). This reconfiguration would not occur if the supporting apparatus was flat: a medial groove, representing about 20 per cent of the supporting apparatus's depth, must have been present. This caused each tooth to rotate relative to its

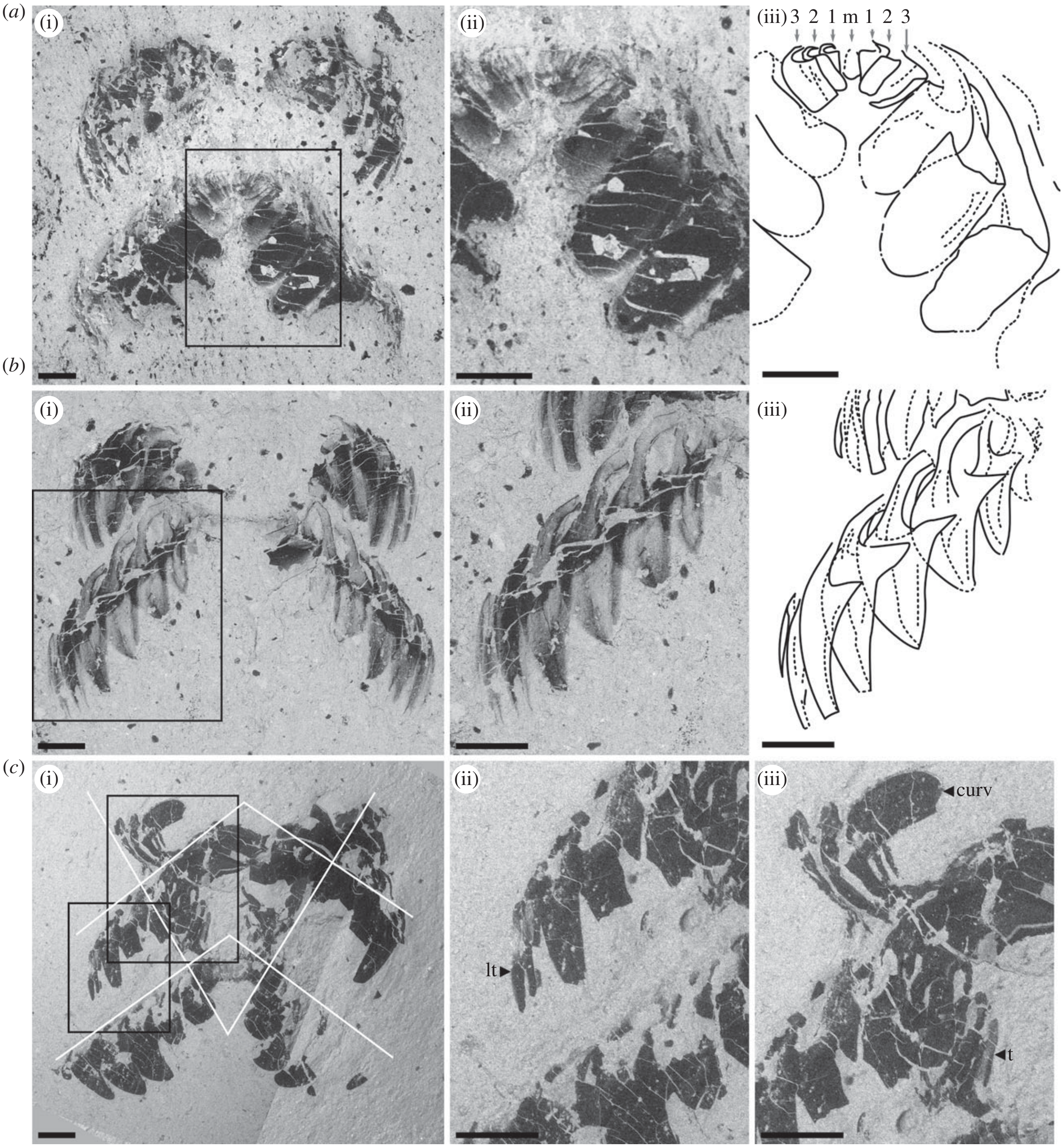

Figure 2. Composite backscatter SEMs (part + counterpart) of *Odontogriphus* teeth. (*a*) ROM 32569, 'scoops' of teeth were originally sub-parallel to bedding, medial tooth (m) flanked on each side by three diminutive lateral teeth (1–3) and further large teeth (not numbered); (*b*) ROM 61516; roots of teeth are not connected, no basal plate joins the teeth; scoops were originally sub-perpendicular to bedding and are now flattened; note thickened margin of each tooth; (*c*) ROM 61515, first tooth row in inverted position; note lateral teeth (lt), curvature of teeth in lateral profile (curv), and thickening of tooth margins (t); white lines emphasize change in chevron angle. Scale bars, (*a–c*) 200 μm.

neighbours as it rounded the end of the supporting apparatus (figure 3*b*). The lateral teeth, like a racer in an outside lane, had further to travel; they would fall back as the chevron rounded the support. This produces the anteriad decrease in total chevron width measured by Caron *et al.* [2], but does not affect the along-chevron distance from the central tooth to the most distal; this measurement, being independent of chevron angle, is not significantly different between the two posterior rows (paired *t*-test, $p = 0.40$, d.f. = 14; data log-transformed). Measured this way, the size of adjacent rows is identical (slope not significantly different from 1, Pearson correlation $p = 0.22$; constrained to pass through origin, d.f. = 12, adjusted $R^2 = 0.9996$).

Wiwaxia's tooth rows (figure 4) differ from those of *Odontogriphus* in a number of respects. Each row consists of a central tooth, flanked on each side by six to 11 medial teeth; larger tooth-rows bear more teeth (adjusted $R^2 = 0.76$; $p \ll 0.001$). Three to five diminutive lateral teeth are sometimes preserved on each side. Rather than chevrons, teeth form an open-based isosceles trapezium. In the resting position, the base angle measures 33° to 61° (mean = 44 ± 9°, $n = 26$; angle significantly smaller than *Odontogriphus*, with two-tailed Mann–Whitney

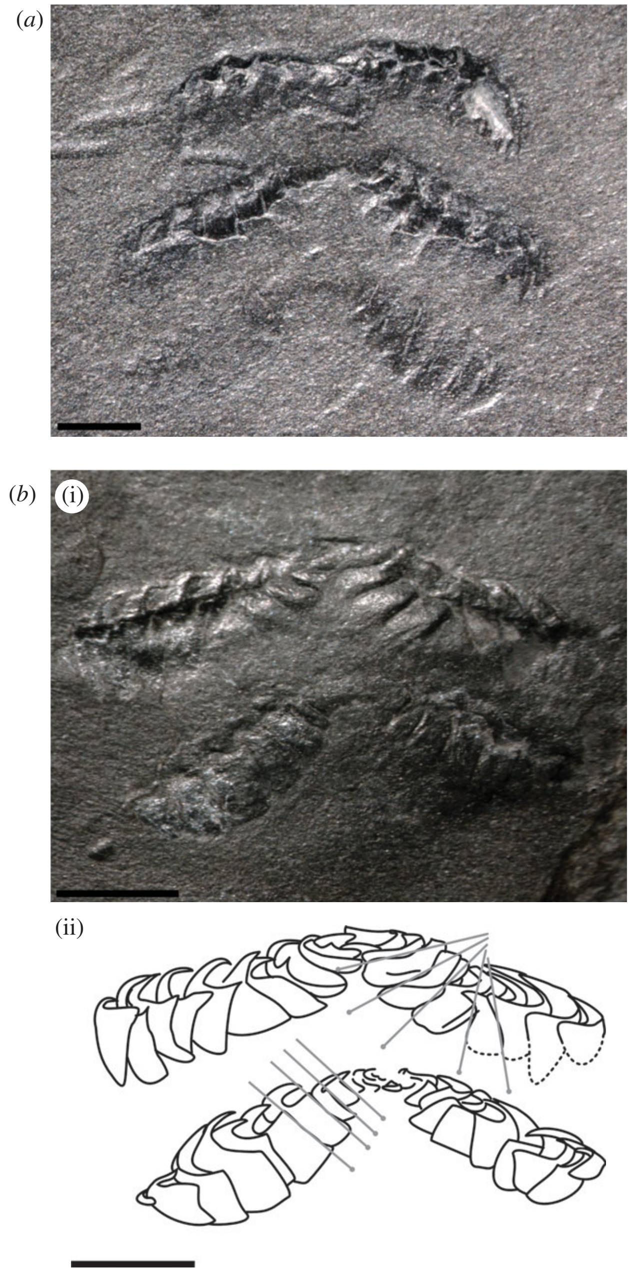

Figure 3. *Odontogriphus* tooth rows. (*a*) ROM 57716, third tooth row is faintly preserved, and has less relief than anterior two rows; teeth retain relief and interrupt the plane of splitting; (*b*) ROM 61700, teeth rotate as the front tooth row passes round the end of the supporting apparatus; grey lines emphasize angle of adjacent teeth. Scale bars, (*a*,*b*) 1 mm.

$p < 10^{-4}$). Smaller specimens are more steeply angled (exponent $= 0.13 \pm 0.05$, $p = 0.02$, adjusted $R^2 = 0.17$), indicating a loose ontogenetic trend towards straighter tooth rows. Only three *Wiwaxia* specimens preserve tooth rows in the active position; once round the end of the supporting apparatus, the top of the trapezoid remains straight as the legs become more steeply angled—denoting a broad medial groove that represents 30 per cent of the support's thickness. As in two specimens of *Odontogriphus* [2], partial tooth rows (recognizable by their morphology, size and composition) are present in the guts of two *Wiwaxia* specimens (figure 5). This indicates that mouthparts were sloughed, swallowed and—judging by their posterior position in the gut—indigestible.

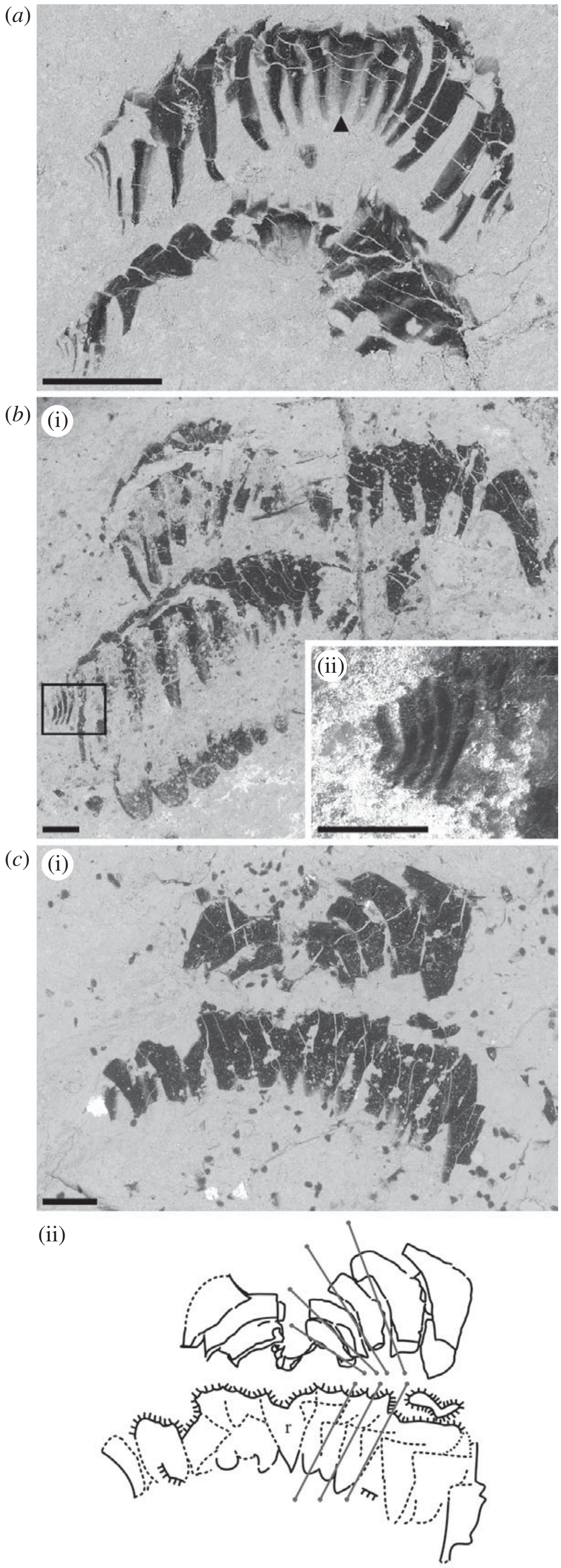

Figure 4. Composite backscatter SEMs (part + counterpart) of *Wiwaxia* tooth rows. (*a*) Smithsonian Institution, National Museum of Natural History (USNM) 277890, dorsal surface, symmetrical central tooth (arrowed) obvious, three lateral teeth; (*b*) ROM 61517, ventral surface, three tooth rows and five lateral teeth; (ii) lateral teeth, SE image; (*c*) USNM 199892, showing rotation of teeth into medial groove; leading tooth row has rounded the end of the supporting apparatus. Grey lines emphasize angle of adjacent teeth. Scale bars, (*a*–*c*) 200 μm.

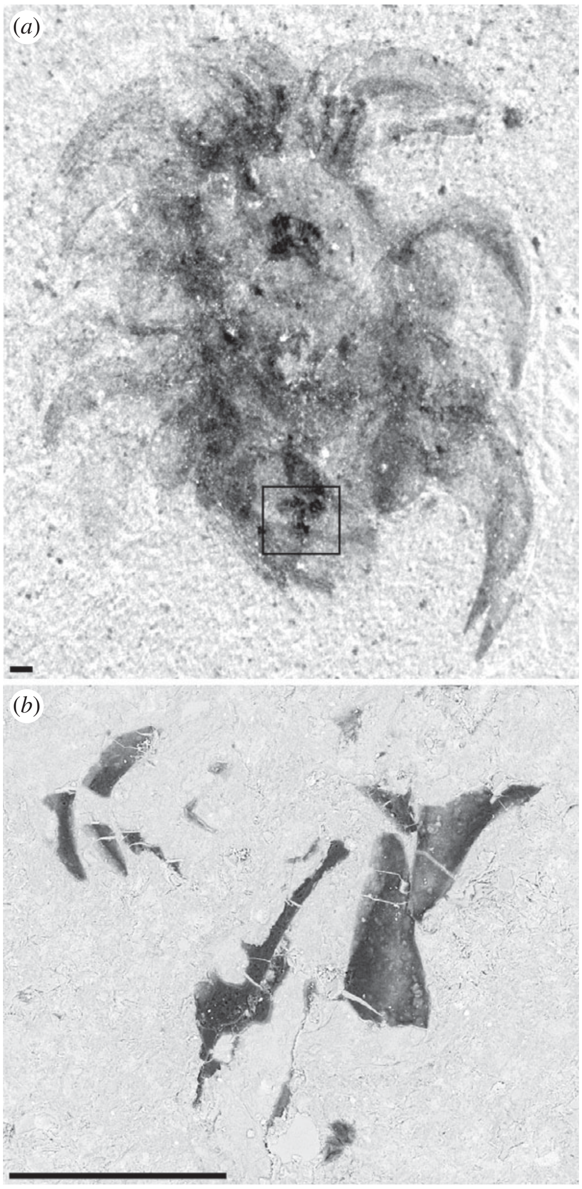

Figure 5. Fragmented mouthparts in *Wiwaxia* gut. USNM 277890. (*a*) Interference image of entire specimen; (*b*) backscatter SEM of boxed area. Scale bars, (*a*,*b*) 200 μm.

(d) *Mouthpart lobes*

Some *Odontogriphus* specimens preserve an internal lobe of resistant tissue on each side of the tooth rows (figure 6*a–c*), usually as aluminosilicate films that silhouette the original carbon. In some cases, original carbon is still present and elicits a backscatter SEM response, suggesting that the structure's original constitution was similar to that of the teeth. The outer margins of the lobes, which are darker and more pronounced, were presumably their toughest or thickest parts; these become progressively more labile towards the rear. The lobes emanate from the front of the support and arch dorsally towards its posterior; their attachment was sufficiently robust to survive post-mortem displacement of the feeding apparatus. The lobes do not invert when tooth rows pass round the end of the supporting apparatus, indicating a fixed position relative to mobile tooth rows. The lobes were originally inclined at a small angle to the vertical: in most cases, they are compressed into a butterfly-shape, but sometimes both are flattened in the same direction. Posteriad of the mouthparts, the margins of the lobes come together and connect to a chevron-shaped feature that is similar in angle and width to the tooth rows, but always lacks teeth or other projections (figure 6*a*,*b*). Given their form, ventro-lateral position and detachment from the tooth rows, the lobes are interpreted as attachment rather than as masticatory structures.

3. DISCUSSION

(a) *Reconstruction*

This study confirms that the *Odontogriphus* and *Wiwaxia* feeding apparatuses (figure 7) comprise two to three equally sized, self-similar rows. Significant extracellular secretion is indicated by the residual three-dimensionality of teeth [8]. As iterated by Caron *et al.* [2,7], the mouthparts comprise symmetrical transverse rows of solid teeth that are distinct from, but embedded in, a radular membrane; the rows pass round the end of a supporting apparatus, are sloughed anteriorly and replaced from the posterior, and contain more teeth when they are larger. But where Caron *et al.* identified two denticulate teeth per row [2,7], this study recognizes each 'denticle' as a separate articulating tooth. The robust lobes preserved in *Odontogriphus* attach to the radula, have thickened margins, become increasingly labile towards the rear and are constructed from the same material (presumably chitin) as the radular teeth; they presumably represent a muscle attachment structure. The supporting apparatus bore a medial groove, causing chevron angle to increase and teeth to rotate as they round its cusp. Chevrons are uniformly sized and directed anteriad while the supporting apparatus is in its resting position; all teeth except the symmetrical central tooth have a uniform shape (even though their silhouette on bedding planes varies with burial angle).

(b) *Interpretation*

This new reconstruction is inconsistent with previous interpretations of the *Odontogriphus* and *Wiwaxia* mouthparts as annelid jaws. A comparison with the dorvilleid polychaetes was founded on the difference in morphology between adjacent tooth rows [5], which this study shows to be a taphonomic feature. Dorvilleids have a single planar pincer-like jaw [14] with teeth in a fixed position [15]; *Odontogriphus* and *Wiwaxia* have multiple, transverse rows containing teeth that rotate relative to one another. In dorvilleids, jaw exuviae are shed laterally and are fainter than functional rows [16]; in *Odontogriphus* and *Wiwaxia*, moulted rows are shed from the front of the apparatus and remain strongly carbonized. Dorvilleids replace moulted jaws with new ones that are substantially (1.4 times) larger [17], but each subsequent tooth row in *Odontogriphus* or *Wiwaxia* is the same size. Tooth shape changes as the dorvilleid jaw grows [16], but never changes in *Odontogriphus* or *Wiwaxia*. *Odontogriphus* and *Wiwaxia* have no equivalent to the permanent (non-moulted) dorvilleid mandible.

Given these barriers to a dorvilleid interpretation, might the single chevron-shaped tooth row in the ampharetid annelids be a better proxy for the *Odontogriphus* and *Wiwaxia* mouthparts [5]? Butterfield [8] no longer considers these jaws to be comparable with multi-rowed apparatuses, and indeed their construction from bilateral

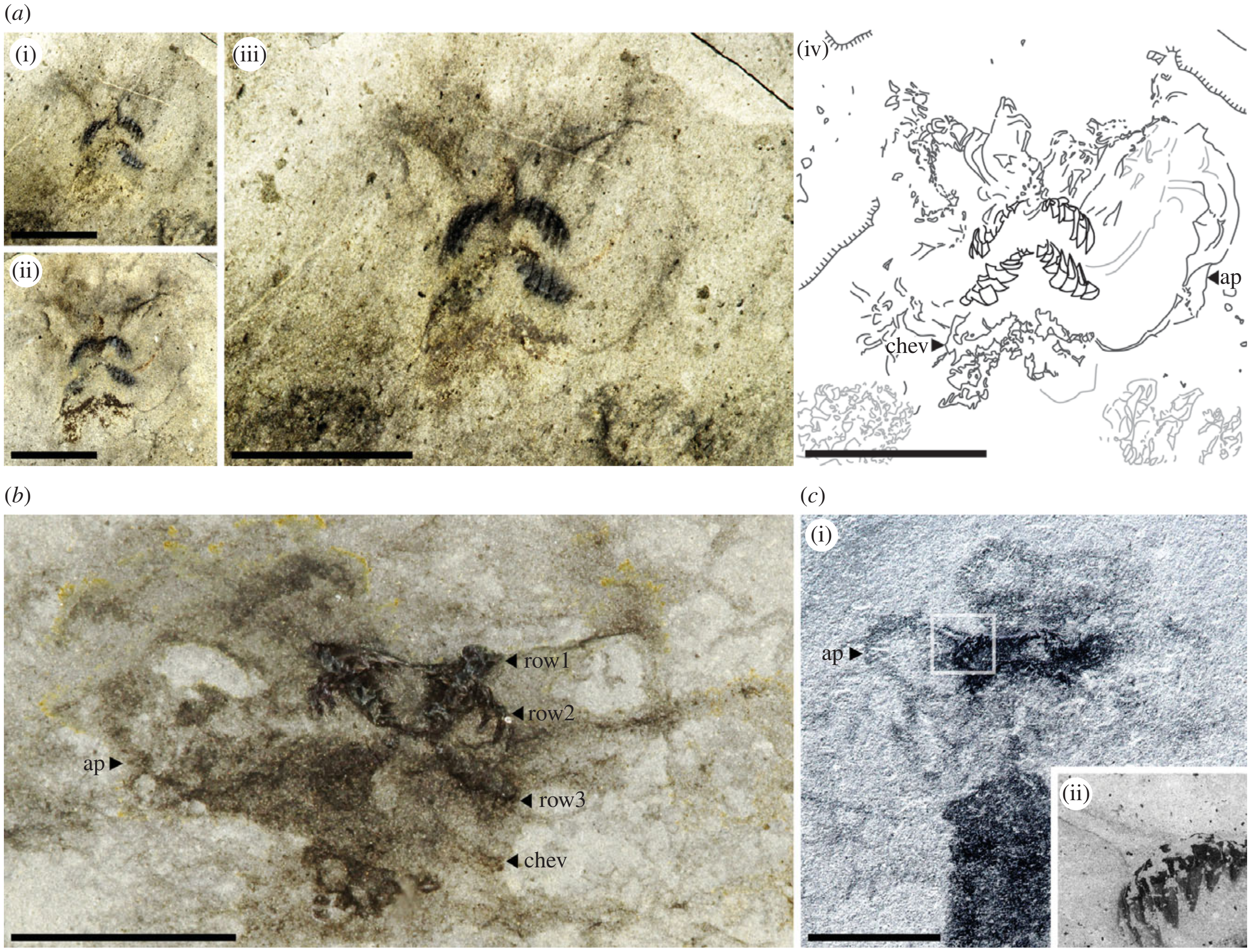

Figure 6. Mouthpart lobes in *Odontogriphus*. (*a*) ROM 61514, showing alary process (ap), which forms a chevron-shaped structure (chev) at the anterior; (*b*) partly decayed specimen ROM 57715; mouthparts show alary process (ap), and faint posterior chevron (chev), first of three rows of teeth (row1–row3) is in an inverted position; (*c*)(i) interference image of ROM 57714, alary process (ap) attached to feeding apparatus; (*c*)(ii) proximal portion of mouthpart lobe: overlay of SE + BSE signals. Scale bars, (*a*–*c*) 5 mm.

series of teeth on the posterior edge of a ventral bulb [18,19] is at odds with the central tooth and anterior placement of the tooth rows of *Odontogriphus* and *Wiwaxia*. Furthermore, I am aware of no ampharetid that moults its teeth.

The similarities between the fossils' mouthparts and annelid jaws are only superficial, whereas the molluscan radula bears a number of specific features [20] that are also present in *Odontogriphus* and *Wiwaxia*:

— a basal membrane: implied in *Odontogriphus* and *Wiwaxia* because isolated feeding apparatuses remain articulated;
— a supporting apparatus with a median groove: indicated by the flexure of rows and the rotation of teeth;
— adjacent tooth rows of similar sizes;
— deciduous teeth: tooth rows are occasionally present in the guts of both *Odontogriphus* and *Wiwaxia*, and the number of tooth rows varies from two to three with no relation to size;
— addition of new tooth rows at the posterior: evidenced by fainter, weakly carbonized tooth rows intermittently present in this position;
— significant extracellular secretion: indicated by the residual three-dimensionality of teeth [8];
— a symmetrical central tooth: establishing each tooth row as a single (not bipartite) entity;
— a robust structure (alary process/hyaline shield) attached to the radula, with thickened margins, increasingly labile towards the rear, and constructed from the same material (chitin) as the radular teeth [20,21]: observed in *Odontogriphus* and inferred in *Wiwaxia*; and
— more teeth per row in larger specimens.

Although the small number of tooth rows in *Odontogriphus* and *Wiwaxia* is unusual among modern molluscs, some juvenile Polyplacophora have three (or perhaps fewer) tooth rows when they begin grazing [22]. The strong morphological overlap between the molluscan radula and the mouthparts of *Odontogriphus* and *Wiwaxia* clearly eclipses their similarities with dorvilleid and eunicid jaws, whose convergent origin is exposed by fundamental differences in construction.

(c) *Comparison with microfossils*

Harvey *et al.* [23] recovered tooth-like elements from acid macerates of the early Middle Cambrian Kaili biota, some of which resemble the teeth of *Odontogriphus* and *Wiwaxia*

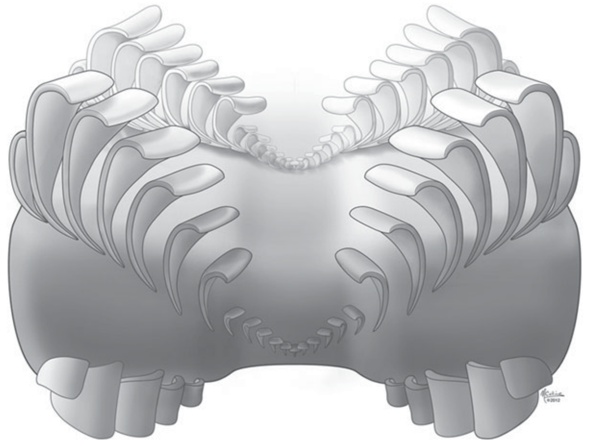

Figure 7. Reconstruction of teeth and supporting apparatus in *Odontogriphus*. Copyright Marianne Collins 2012.

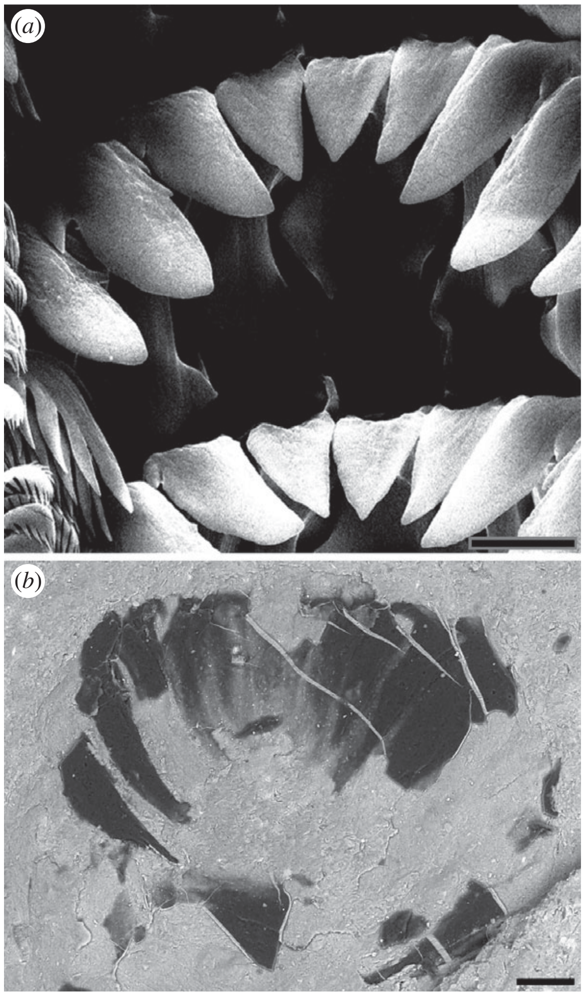

Figure 8. Comparison with modern radula. (*a*) Radular tooth rows in the larval particle-feeding gastropod *Haliotis discus hannai* [30], courtesy T. Kawamura; (*b*) tooth row in *Wiwaxia*, USNM 200101. Scale bars, (*a*) 10 µm; (*b*) 50 µm.

in outline and in having thickened margins, but the lack of articulated apparatuses impedes a detailed comparison.

A resemblance can also be found with certain boot-shaped and fibrous elements from Early Cambrian radulae [8], which also have a fibrous (microvillar?) construction and imbricate to form a bilaterally symmetrical array. However—notwithstanding tooth morphology—these rows lack a symmetrical central tooth, are very closely spaced and have many (up to 29) teeth; so they do not merit close comparison with *Odontogriphus* or *Wiwaxia*.

Scoop-shaped teeth from the Mount Cap formation display pointed roots and thickened margins, and take a strikingly similar formation when articulated [24]. These teeth, which have an internal fibrous microstructure and are found in association with *Wiwaxia* sclerites, may well have belonged to an *Odontogriphus*- or *Wiwaxia*-like organism.

(d) *Radula and ecology*

The diet of many molluscs is constrained by radular morphology [25], but radulae can also adapt to available food sources—either by plasticity [26] or natural selection [27]. Accordingly, the radula provides a rich ecological signal.

Although the match between radula and foodstuff is not always exact, some patterns persist throughout the Mollusca and constrain the *Odontogriphus* or *Wiwaxia* diet. All molluscan macroalgivores have a pair of pronounced gouging teeth with which to incise their food [28]; if their foodstuff is calcified, these teeth are inevitably mineralized (although the converse relationship does not hold). Long, thin, raking teeth are necessary to sweep up filamentous algae, and all gastropods that feed on calcified or leathery algae, or on meat, have serrated teeth. To rasp hard substrates (such as calcifying algae) requires a file-like radula with teeth in a fixed relative position. When teeth rotate relative to their neighbours, as in *Odontogriphus* and *Wiwaxia*, the radular function is generally limited to sweeping food from a surface, abrading soft tissue or excavating sediment [28,29].

Radulae that comprise morphologically uniform, unornamented, shoehorn-shaped teeth (figure 8) are today found in particle-feeding gastropods, some extant monoplacophorans (*Neopilina*) and chitons—although in the latter case the marginal and central teeth are reduced to plates. *Neopilina* and chitons are a promising ecological analogue to *Wiwaxia* and *Odontogriphus*. Some chitons feed on sponges [31], but sponge spicules (although indigestible) are never preserved in the *Odontogriphus* or *Wiwaxia* digestive tract. Most chitons, like *Neopilina*, are deposit feeders [32,33]—reflected by the substantial radular musculature, a limited number of teeth (less than 20) per row and teeth that rotate relative to their neighbours [28]. These traits are shared by *Odontogriphus* and *Wiwaxia* (the musculature, at least in *Odontogriphus*, indicated by the large alary process): this substantiates previous speculation [1] that the organisms were deposit feeders.

(e) *Ancestral molluscan radula*

Even relatively minor changes to a species' radula can have dramatic ecological consequences [34], and the rise of radula-driven herbivory likely contributed to the Cambrian substrate revolution. Unfortunately, the organ's origin is ill-constrained. The first fossil evidence of a radula-like organ comes from scrape-marks left by the putative Ediacaran mollusc *Kimberella* [35,36], but radulae themselves are rarely fossilized. The oldest fossil radulae (dating to the Early Cambrian) already share derived characters associated with aplacophorans and gastropods [8]. Like those of *Odontogriphus* and *Wiwaxia*, these resemble flexoglossate

radulae with independently rotating teeth—contrasting with the parallel grooves scratched by *Kimberella* [36], which denote stereoglossy [29].

The unsettled status of molluscan phylogeny means that extant taxa do little to constrain the ancestral radula. Wingstrand, who interpreted the radulae of chitons and extant monoplacophorans to represent the ancestral format [37], postulated that paired fluid-filled vessels created a groove in the radular support (resulting in flexoglossy). He imagined a small number of teeth on each row: a small medial tooth flanked by larger hooked teeth, then a comb-shaped tooth and diminutive marginal teeth [37]. But if the Aplacophora are interpreted as basal, a bipartite and distichous reconstruction results, with no median tooth or tooth rotation [6]. Recent analyses generally recover a derived position for aplacophorans [38–43], and molecular phylogenies imply that the ancestral radula bore multiple teeth per row [43]. Taking *Odontogriphus* and *Wiwaxia* to be more basal than the Aplacophora, the ancestral mollusc bore a functionally flexoglossate, unipartite radula with multiple regions of distinct teeth and a symmetrical central tooth.

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