A new species of early Cambrian arthropod reconstructed from exceptionally preserved mandibles and associated small carbonaceous fossils (SCFs)

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Abstract: Mandibulate arthropods (myriapods, hexapods and crustaceans) account for a major component of extant animal diversity but their origins remain unclear. Here, we re-examine the record of exceptionally preserved arthropodan microfossils, including mandibles, from the lower Cambrian (Stage 4) Mount Clark Formation, Northwest Territories, Canada. The assemblage comes from a single drillcore horizon and occurs as thousands of small carbonaceous fossils (SCFs) representing disarticulated body parts. The mandibles occur as isolated molar surfaces with an elongate outline, a heavy setal fringe, and a subtle right–left asymmetry. These are sufficiently distinctive to diagnose a new genus and species of arthropod, Masticaris fimbriata. Co-occurring SCFs include diverse appendage lobes and ventral body fragments, along with spines and setae assignable to 53 morphological categories and occurring either singly or in arrays, including filter plates. Most are plausibly interpreted as belonging to the feeding apparatus of M. fimbriata. The mandibles and filter plates correspond to those in extant pancrustaceans, particularly branchiopods, although the mouthparts of some more basal Cambrian arthropods raise the possibility of convergent feeding adaptations. Overall, anatomical and taphonomic continuity with younger SCFs suggests that M. fimbriata belongs to an early pancrustacean radiation that is still largely cryptic in the fossil record. More generally, the assemblage provides an inventory of fine-scale cuticular specializations in early Cambrian arthropods that prefigure the trophic versatility and ecological dominance of crustaceans in the modern marine fauna.

Key words: Cambrian, mandible, small carbonaceous fossils, Pancrustacea, palaeoecology, Arthropoda.

The Cambrian fossil record preserves a rich diversity of arthropods, from a time when the major lineages were acquiring their defining characteristics. Despite this, we still lack a coherent account of the early evolution of mandibulate arthropods, the group containing crustaceans, hexapods and myriapods. Modern mandibulates share a suite of clear synapomorphies, and their monophyly is supported in all modern molecular analyses, including a well-established sister-group relationship between myriapods (millipedes, centipedes etc.) and pancrustaceans (paraphyletic crustaceans plus hexapods, i.e. insects and their relatives) (e.g. Edgecombe 2020). However, the identification of mandibulates among Cambrian arthropods has not proved straightforward, and has a convoluted history. Even with a wealth of discoveries in recent years, difficulties remain in reconciling the information from fossils preserved in different taphonomic modes.

Various superficially crustacean-like arthropods occur among Cambrian macrofossils, and for much of the twentieth century these were ‘shoehorned’ into modern groups. However, all were later relegated to positions in the euarthropod stem (i.e. outside the least inclusive clade containing modern mandibulates, chelicerates and pycnogonids), based on their apparently plesiomorphic head structures (e.g. Budd 2002, 2008; Legg et al. 2012). More recently, however, a substantial number of Cambrian taxa (more than 10 genera) have been reinterpreted as total-group mandibulates based on newly resolved details of the head. Proposed stem-mandibulates include the ‘hymenocarines’, a suite of bivalved arthropods known principally from the Burgess Shale and preserved as detailed but largely flattened compression fossils (Aria & Caron 2017; Vannier et al. 2018; Izquierdo-López & Caron 2021). Elsewhere, the use of computed tomography (CT) to reconstruct partially three-dimensionally preserved specimens from the Chengjiang biota has revealed a pancrustacean-like head structure in Ercaicunia (Zhai et al. 2019a). In addition, the identification of the
Cambrian to Triassic euthycarcinoids as stem-group myriapods based on decisive new data from the Devonian Rhynie Chert (Edgecombe et al. 2020) has fuelled a reinterpretation of the fuxianhuiids, a major early Cambrian group, as mandibulates with possible myriapodan affinities (Aria et al. 2021). There is considerable debate over these proposed phylogenetic scenarios, however. In particular, the apparent absence of (second) antennae in various candidate mandibulates, and uncertainty over the identity and position of the labrum, raise major questions about how the arthropod head and brain were reorganized during the establishment of the major crown groups (e.g. Edgecombe 2017, 2020; Budd 2021).

Elsewhere in the Cambrian fossil record, Orsten-type assemblages of minute (<2 mm) arthropods have long been recognized as preserving a diversity of mandibulates, even if the individual taxa, many of which show larval characteristics, have proved hard to place in the mandibulate tree (e.g. Wolfe & Hegna 2014). Another complication is the shifting phylogenetic context, so that characters proposed to illuminate the emergence of crown-group crustaceans must have originated in the stem-group of Pancrustacea or Mandibulata in the context of modern molecular phylogenies (reviewed in Edgecombe 2020). Nevertheless, several Orsten-type taxa possess a straightforward complement of crustacean-type head appendages; that is, a uniramous antennule followed by biramous antennae, mandibles, one or two pairs of maxillae, and a labrum shielding the mouth (e.g. Walossek et al. 2007).

Another source of evidence on early mandibulates comes from small carbonaceous fossils (SCFs), which, as the name suggests, are carbonaceous compression fossils on a small scale. In general, SCFs are too small to be observed on bedding planes but are larger or more delicate than standard palynomorphs, and require low-manipulation acid extraction to be isolated from their rock matrix (Butterfield & Harvey 2012). SCFs are more widespread than their macroscopic Burgess Shale-type counterparts, both geographically and in terms of depositional environment, presumably because they require less restrictive conditions for burial and preservation. However, there is a taphonomic trade-off: although arthropodan SCFs can preserve cuticular structures to an unprecedented sub-micron resolution, they typically occur as highly disarticulated body parts, frustrating direct comparison to whole-body fossils. Even so, a diverse array of arthropodan body parts have been identified among Cambrian SCFs, including mandibles, the defining ‘jaws’ of mandibulates (Harvey & Butterfield 2008; Harvey et al. 2012; Harvey & Pedder 2013; Wallet et al. 2021). SCFs seem to record a largely cryptic Cambrian radiation of phylogenetically and anatomically derived mandibulates, not evident in other taphonomic modes. Inevitably, each mode will be influenced by a distinct balance of preservational controls, including loss or retention of features in decay and preservation, sampling of particular body sizes or ontogenetic stages, and representation of different ecologies and environmental settings.

A major advantage of SCFs is the exceptional preservation of cuticular structures such as spines, setae and other ornamentation. Features smaller than 1 µm are often clearly resolvable using transmitted light microscopy and scanning electron microscopy (SEM). The fine-scale ornamentation of the mandible, in particular, can be a rich source of phylogenetic information. Therefore, resolving the fine structure of the perioral appendages in candidate Cambrian mandibulates is of key importance. Mandibular features are well resolved in many Orsten fossils (e.g. in Rehbuchiella; Walossek 1993), but in Cambrian macrofossils, including many of the proposed hymenocarines, the region immediately surrounding the mouth tends to be obscured by superimposed head sclerites and appendages. Despite their disarticulated condition, SCFs can reveal the detailed characters of mandibles derived from individuals with macroscopic dimensions, providing a crucial extension of the dataset from small-bodied Orsten individuals (e.g. Harvey & Butterfield 2008; Harvey et al. 2012).

More generally, the fine-scale features preserved in arthropodan SCFs can yield new insights into functional capabilities and, in turn, palaeoecology. Most assessments of Cambrian arthropod modes of life have relied on overall body and limb shape to distinguish the probable modes of locomotion and feeding (e.g. Briggs & Whittington 1985). Where preservation allows, details of the shapes and ornamentation of limb articles enable quantitative biomechanical analyses of probable feeding styles and efficiency (e.g. Bicknell et al. 2021). At a finer scale, the forms and positions of cuticular projections allow inferences about their mechanical and sensory capabilities, in turn informing reconstructions of behaviour, both for Orsten-type fossils (e.g. Walossek 1993) and, in exceptional cases, for Burgess Shale-type macrofossils (e.g. Strausfeld 2016). The unprecedented resolution of preservation in SCFs allows an extra level of analysis of the functions of individual cuticular projections and the arrays and armatures in which they occur (e.g. Harvey et al. 2012). The challenge is then to establish how the SCFs relate to whole-body Cambrian fossils. At least in principle, SCFs can bridge the gap between Orsten-type small-bodied forms and macroscopic Burgess Shale-type taxa, providing a much more comprehensive knowledge of Cambrian arthropod ecologies.

The aim of this study is to document fully an exceptionally preserved assemblage of arthropodan SCFs from the lower Cambrian (Stage 4) Mount Clark Formation (in previous publications assigned to the Mount Cap Formation) of northwest Canada. In the initial report,
Butterfield (1994) suggested that the isolated spines and setae in the SCF assemblage were derived from a filter-feeding crustacean perhaps 10 mm long. Harvey & Butterfield (2008) subsequently identified mandibular molar surfaces, the details of which supported a phylogenetic position among crown-group pancrustaceans, and argued for both a larger body size and a more sophisticated feeding ecology. Here, we provide a comprehensive description of the Mount Clark arthropod SCFs in order to constrain the phylogenetic position and palaeoecology of the constituent taxon or taxa, and to provide a comparative framework for the description of arthropodan SCFs more generally. Our results bear on the interpretation of Cambrian arthropods preserved across all taphonomic modes.

**MATERIAL AND METHOD**

The material described here comes from a thin (c. 50 mm) horizon of dark, fine-grained slightly pyritic mudstone at a depth of c. 1351 m in cored well Bele O-35 (PCI Canterra Bele O-35, 300/O-35-6640-12 615/0) from the Colville Hills area, Northwest Territories, Canada (66°34′58.14″N, 126°21′32.11″W; see Butterfield 1994; Harvey & Butterfield 2011). Although previously reported as belonging to the lower Mount Cap Formation, it is now recognized as the Mount Clark Formation, occurring some 7 m below the first appearance of carbonate-rich units that define the base of the Mount Cap Formation (see Herbers et al. 2016, fig. 6). The boundary between the two formations is regionally diachronous, ranging in age from Bonnia–Olenellus Zone to Albertella Zone (Herbers et al. 2016). Within Bele-O35 the fossiliferous horizon at 1351 m is constrained by the presence of the olenellid trilobite Wanneria c. 20 m higher in the succession (Butterfield 1994), along with Bonnia–Olenellus Zone trilobites more generally through the upper Mount Clark Formation (Sommers et al. 2020, fig. 12). In terms of age, olenellids by convention characterize Cambrian Stage 4, which is undefined at the base but is suggested in the international chronostratigraphic scheme to range from an estimated 514.5 Ma to the base of the Miaolingian Epoch at 509.0 Ma (Peng et al. 2020). Recent radiometric dating, however, has constrained the extinction of olenellids in southwest Laurentia to c. 506.5 Ma (Karlstrom et al. 2020; Sundberg et al. 2020). Thus, the Mount Clark SCF assemblage can be considered to belong to Cambrian Stage 4 with an age no younger than 506.5 Ma.

Overall, the Mount Clark and Mount Cap succession records deposition in shoreface to offshore environments in a semi-enclosed epicontinental basin (the Colville Basin; Sommers et al. 2020). The lower part of the Mount Clark Formation is dominated by sandstones, recording storm-influenced shoreface deposits from the initial Cambrian transgression onto eroded Proterozoic basement, whereas the finer-grained interval sampled in Bele O-35 locally records offshore and lower shoreface deposition (Herbers et al. 2016; Sommers et al. 2020). Palaeobiologically, the Mount Clark–Mount Cap succession has yielded several instances of exceptionally preserved micro- and macrofossils, both from drillcore (Butterfield 1994) and from outcrop in the Mackenzie Mountains, some 200 km to the south (the ‘Little Bear biota’ of the Mount Cap Formation; see Butterfield & Nicholas 1996; Harvey & Butterfield 2011). Even so, the horizon at 1351 m in Bele O-35 is unique in its abundance and diversity of arthropodan SCFs, pointing to local depositional and diagenetic conditions favouring exceptional preservation.

Around 150 g of the fossiliferous mudstone (in eight subsamples) were disaggregated in hydrofluoric acid (HF) and gently rinsed on a 60 μm screen. The water-suspended residues were then inspected under a binocular stereoscope, and fossils picked individually using a fine pipette (for further details of the method, see Butterfield & Harvey 2012). In addition to the arthropod SCFs, the Bele O-35 assemblage includes Wiwaxia sclerites, molluscan radulae (Harvey & Butterfield 2011) and smooth or punctate cuticle fragments of indeterminate origin. The arthropod SCFs are identified by their diagnostic cuticular projections (spines and setae) and smooth rather than fibrous surface texture. They are preserved as flattened, entirely carbonaceous cuticle fragments, sometimes with void-filling euhedral pyrite crystals (Butterfield 2003, fig. 1) and/or adhering pyrite framboids, which commonly imprint or disrupt the carbonaceous film. The absence of articulated fragments on bedding planes and the frequent occurrence of pre-compactional folding or curling indicates that the fragments had disarticulated prior to final burial; delicate specimens may have become further disarticulated during laboratory processing.

A total of 2882 arthropod SCFs were mounted for either light microscopy (2624 specimens on 232 glass slides) or SEM (258 specimens on 44 aluminium stubs). All of the fossil material is stored at the Geological Survey of Canada (GSC), Ottawa, Ontario, Canada, with figured specimens numbered as indicated in the figure captions (Table S1). Transmitted light micrographs have been processed using stacking software (Combine CP and Adobe Photoshop) to achieve a single focal plane. Some scanning electron micrographs are composite images based on adjacent tiles.

**Institutional abbreviation.** GSC, Geological Survey of Canada, Ottawa, Ontario, Canada.
SYSTEMATIC PALAEOONTOLOGY

The highly disarticulated nature of the Mount Clark arthropods presents a taxonomic dilemma. Previously the material has been described anatomically, without taxonomic assignment (Butterfield 1994; Harvey & Butterfield 2008). However, the discovery of similarly preserved but morphologically distinct crustacean microfossils in the Earlie–Deadwood succession of western Canada (Harvey et al. 2012) provides the impetus for a more formal taxonomic framework that emphasizes differential diagnosis. The ultimate aim is to establish the true biological diversity of arthropods represented by the disarticulated SCFs, and simply describing the material under open nomenclature is unlikely to advance knowledge in this direction. The solution we propose for the Mount Clark material is to erect a new arthropod taxon based primarily on its mandibular ornamentation. Of all the body parts preserved in the assemblage, the mandibles provide the most reliable source of species-level information. They are intricate, character-rich body parts that occur in reasonable numbers (N = 71), allowing ontogenetic and other intraspecies variation to be delimited, assuming comparable limits in living crustaceans. They also provide information on phylogenetic affinity and body size. As such, it is possible to gain substantial knowledge of the original biological population, and the species to which it belongs, through the mandibles alone.

The immediate value of establishing the new taxon will be in distinguishing the Mount Clark specimens from other fossil mandibles. Ideally, of course, the new taxon will become more completely known in future via the discovery of articulated SCFs linking body parts together, repeated patterns of co-occurrence, and/or high-resolution imaging of macrofossils with comparable mandibles in situ. We consider the possibility that various co-occurring body parts in the Mount Clark assemblage derive from the same new taxon (and indeed our analysis supports this view) although as a conservative measure, the diagnosis relies only on the mandibles. Importantly, we do not create names for other body parts in the assemblage but assign them to informal form-categories. Even for the mandibles, we do not wish to create a (para)taxonomy of isolated parts (see Bengtson 1985), which in any case is prohibited by the ICZN, but rather a natural biological classification, as advocated for other disarticulated fossil mouthparts such as conodonts (Jeppsson & Merrill 1982) and scolecodonts (Eriksson et al. 2000). A further complication, not faced to the same extent with these other groups, involves the markedly different taxonomic information and preservation potential among arthropod exoskeletal elements: mandibles can diagnose species, but tergites and podomeres (for example) probably cannot, and ‘softer’ skeletal parts might be missing entirely. To that extent, the challenges posed by arthropodan SCFs are perhaps most analogous to the disarticulating parts of fossil plants. The solution in palaeobotany is to distinguish ‘unshared organ-species’ (autapospies, corresponding to a single biological species) from less diagnostic ‘shared organ-species’ (form-species) (e.g. Bateman & Hilton 2009). Rather than propose such a complex system of names for arthropodan SCFs, we suggest a mandible-based name that applies to the whole organism, as has been applied to, for example, fish known principally from isolated teeth (Duncan 2003). The benefits for understanding Cambrian arthropod palaeobiology are likely to outweigh any future work required to synonymize names, should discoveries of exceptionally preserved, fully articulated material become available.

Phylum ARTHROPODA Siebold, 1848 (sensu Hegna et al. 2013)

Genus MASTICARIS nov.

LSID. urn:lsid:zoobank.org:act:07EDB726-A34B-4374-9F1F-919F2AA13997

Derivation of name. From the Latin mastico- (chew) and caris (shrimp), in reference to the well-developed jaws.

Type species. Masticaris fimbriata sp. nov.

Diagnosis. As for type and only known species.

Masticaris fimbriata sp. nov.

Figures 1, 2

LSID. urn:lsid:zoobank.org:act:EFA1905D-A45E-4D2C-8797-F2358C170654

Derivation of name. From Latin, fimbriatus (fringed), in reference to the prominent setal fringe on the mandibular molar surface.

Holotype. GSC 142738, a complete right molar (Fig. 2D).

Paratypes. GSC 142736, a left molar, anterior part (Fig. 2A, B); GSC 34938, a right molar, anterior part (Fig. 2E–H); and GSC 34936, a right molar, posterior part (Fig. 2I–M).

Material. 71 complete or partial mandibular molar surfaces, including 23 mounted on SEM stubs and 48 on glass slides (Table S1). Associated arthropodan microfossils are described separately (see below).

Diagnosis. An arthropod with a mandible bearing an elaborate grinding surface on the mandibular pars molaris; molar region D-shaped, elongate (3–5-fold longer than wide), with extensive setal fringe and posterior and anterior setal tufts; fringe-bounded region with up to several hundred incomplete transverse rows of scales merging with a longitudinal unornamented zone; marginal postero-dorsal region with a contrasting ornamentation of short spines and setae; left and right molars asymmetrical, with fringe and scales more strongly expressed dorsally on the left and ventrally on the right.

Description. The Mount Clark molars are preserved detached from the rest of the mandible, as single-walled sheets of cuticle with elongate–ovoid or D-shaped outlines that are delimited by a setal fringe that grades into tufts of long setae at either end.
Ten specimens extend on one side into a skirt of cuticle with sparsely distributed setae (e.g. Fig. 1A–D). Many specimens are deformed by taphonomic folding, twisting or foreshortening (e.g. Fig. 1A, F, G). Comparatively undeformed and complete specimens have ornamented molar regions that range from c. 190–650 μm in length (mean, 420 μm; SD, 177; n = 7) and c. 40–180 μm in width (mean, 109 μm; SD, 32; n = 42), with approximate length : width ratios of between 3 (e.g. Fig. 2D) and 5 (e.g. Fig. 1H). No fragmentary or deformed molar specimens attributable to *M. fimbriata* fall definitively outside of this range. A large fragment with an incomplete width of 230 μm has a distinct ornamentation and may represent a different taxon (see Harvey & Butterfield 2008, fig. S2b, c). Specimens with apparent length : width ratios of c. 5.5–6 (e.g. Fig. 1A) appear transversely foreshortened along at least part of their length, suggesting that these higher values are likely to be artefacts of taphonomic distortion.

The fringe-bounded region bears a complex and characteristic ornamentation of transverse lineations, typically 2–4 μm in width, which are constructed from rows of minute cuticular scales (Fig. 2). A small specimen (Fig. 1H) has around 55 scale rows, whereas larger specimens have more than 150 (e.g. Fig. 1B). The ornamentation is regular across most of the molar surface but is modified towards the narrow ends. In general, the scales in each row lengthen towards the robust margin, where they grade into the fringing setae, and shorten towards the centre of the molar region, becoming confluent with an unornamented region (Fig. 2). The scales are borne on ridges of cuticle that deepen towards the robust margin where they are developed as imbricating lamellae (Fig. 2B, I). Towards the central molar region, the scales take the form of rectangular projections with rows of rounded, submicron-scale humps (Fig. 2F, H). Towards the robust margin, the scales grade progressively into palmate forms with finger-like projections, then into stalked forms with long, irregularly bifurcating filaments, and finally into long, robust setae with irregular setule-like branches that occasionally bifurcate (Fig. 2B, G, I).

The fringe of the opposite long margin is less strongly developed and bears more gracile setae with comparatively short and sparse side branches (Fig. 2M); this fringe is not obviously confluent with scale rows except at one narrow end of the molar region (e.g. Fig. 1B, towards the ‘top’). In contrast to the prevailing scaly ornamentation, a narrow marginal zone at one end of the molar surface bears short, robust spines and simple setae (e.g. Figs 1B, 2J, L).

**Remarks.** The detailed preservation of the fossil molars allows the reconstruction of their orientation in life, by reference to equivalent structures in modern crustaceans. The anterior–posterior polarity of the molars is shown by the orientations of their setal tufts, which are directed outwardly (away from the molar region) at the anterior end (i.e. towards the mouth), but inwardly at the posterior end (cf. Mura 1996). Following from this, the more-curved and less-curved margins are assumed to...
be dorsal and ventral, respectively (e.g. Tyson & Sullivan 1981; = posterior and anterior; Edgecombe et al. 2003). Oriented in this way, it is possible to distinguish right- and left-handed molars by a subtle asymmetry in ornamentation, which is seen clearly in SEM view, and is recognizable in specimens mounted for light microscopy after accounting for their ‘way up’ on the slide (summarized in the schematic diagram, Fig. 3). The pattern of variation is consistent across at least 12 well-preserved specimens: five left molars (Figs 1A–D; 2A–C), and seven right molars (Figs 1E–H, 2D, E, J). The more robust fringe, and therefore the most prominent scaly region, is situated dorsally on the left mandible but ventrally on the right (Fig. 3). The ventral left fringe is moderately well developed and confluent with scale rows anteriorly (e.g. Fig. 1B), whereas the dorsal right fringe is notably weak (e.g. Fig. 1E). In contrast, the fringing skirt of cuticle, where present, is consistently located on the ventral margin, and the region of differentiated spiny ornamentation always occurs posteriorly, extending part way along the dorsal margin (Figs 1B, 2J, L).

No other part of the mandible has been identified in the Mount Clark assemblage. A specimen that appears to show a molar surface in situ on a larger cuticle fragment was figured by Harvey & Butterfield (2008, fig. S2a), although its outline and projections are difficult to reconcile with a mandibular identity and it probably represents a chance superposition of unrelated fragments.
Orsten-type fossils, two isolated mandibles assigned to the Mount Clark molars and other Cambrian SCFs. Among differences support at least species-level distinctions between fringes, larger size, and a contrasting pattern of asymmetry; they exemplify in having a more elongate shape, prominent setal et al et al. of western Canada (Harvey et al. 2008). SCFs have been reported from the middle Cambrian (Dru- mian) Marjum Formation of Utah (Aria & Caron 2017, extended data fig. 8) have perioral appendages with molar-like lineated regions. Equivalent structures are possibly present, but less well preserved, in the closely related Tokummia (Aria & Caron 2017, fig. 2d, f). Whether or not these structures are homologous to mandibular molars (see Discussion section), they lack the fringed margin seen in M. fimбриа (Contrasting toothed margins are observed on the perioral mouthparts of Waptia (Vannier et al. 2018, fig. 8) and fuxianhuiids (e.g. Yang et al. 2018, fig. 3f, g), whatever the limb identity; the putative mandibles of Ercaticunia, a small-bodied taxon imaged using micro-CT (Zhai et al. 2019a, fig. 2C), are too poorly preserved to show features of the gnathal edge.

Among extant mandibulates, a lineated scaly molar is well developed in various myriapods, basal hexapods, and branchiopod, malacostracan and remipede crustaceans (Edgecombe et al. 2003); a finely divided molar is also present in certain cephalocarid crustaceans (e.g. Carcupino et al. 2006) and ostracods (Richter & Kornicker 2006). Among these groups, the molars of branchiopods, especially anostracans, are most similar to the fossils: they commonly share a simple elongate D-shaped outline, a large number of scale rows increasing through ontogeny, a regular pattern of mostly unilateral length variation in the scales, and a field of differentiated spiny ornamentation extending obliquely along the dorsal margin from the posterior end (e.g. Ociosynska-Bankierowa 1933; Fryer 1983; Mura 1991, 1996; Tyson & Sullivan 1981; Mura & Del Caldo 1992, 1993; Peterson & Rosowski 1994; Davoodi et al. 2009; Hegna & Lazo-Wasem 2010). Individually these characters are not unique to anostracans because broadly comparable molars occur widely among branchiopods, including in spicicaudatans, cyclasteri- dans and cladocerans (Richter 2004), and in the Devonian Rhynie Chert branchiopod fossils Lepidocaris (Scourfield 1926; Fryer 1985) and Castracollis (Fayers & Trewin 2003).

The pattern of molar asymmetry in M. fimбриа provides an additional character for comparison. Among extant pancrus- taceans, asymmetric molar surfaces are characteristic of various branchiopods, eumalacostracans and lepismatic hexapods (Edgecombe et al. 2003; Richter 2004). The fossil molars resemble various branchiopods (including many anostracans) in having a strong ventral fringe on the right molar (e.g. Mura 1996), although the combination with a strong dorsal fringe on the left (Fig. 3) appears to be unique. The phylogenetic implications of the molar morphology in M. fimбриа are explored in the Discussion section below.

Because larger individuals have larger mandibles, the fossil molars can also be used to reconstruct the overall body size of M. fimбриа. Scaling relationships between molar length and body length imply a mature body length of at least 10 mm and perhaps more than 50 mm, depending on the comparative model (Harvey & Butterfield 2008, fig. S2). Using extant anostracan branchiopods as an analogue, which may be most appro- priate given the shared elongate proportions of their molars, the

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**FIG. 3.** Simplified schematic reconstruction of the mandibular molar surfaces of Masticaris fimбриа gen. et sp. nov. The shading represents the development of a stronger setal fringe on the dorsal margin of the left molar and on the ventral margin of the right molar, defining a right–left asymmetry. Anterior and posterior setal tufts are omitted.

In many extant crustaceans, patterns of variation in fine-scale molar ornamentation can be useful in distinguishing species (e.g. Edwards 1980), although in others, intraspecies variation is high compared with interspecies variation, and distinctions can be made only at the genus level or above (e.g. Mura & Del Caldo 1992; Mura 1996). Even so, the population of Mount Clark molars is parsimoniously reconstructed as representing a single species after accounting for ontogenetic range (addition of scale rows), right–left asymmetry (in scale and fringe distribution) and taphonomic variation (resulting in a range of length : width ratios). The single exception is the large fragment noted above, which has larger (7 μm) scales without divisions (Harvey & Butterfield 2008, fig. S2b); it may represent a divergent morphology characteristic of a later ontogenetic stage, or a separate taxon.

Broadly comparable mandibular molar surfaces preserved as SCFs have been reported from the middle to late Cambrian (Miaolingian and Furongian series) Earlie–Deadwood succession of western Canada (Harvey et al. 2012), and from the lower Cambrian (Series 2) Buen Formation of Greenland (Wallet et al. 2021). The Mount Clark molars differ from the Deadwood examples in having a more elongate shape, prominent setal fringes, larger size, and a contrasting pattern of asymmetry; they lack the toothed margin present in the Buen molars. These differences support at least species-level distinctions between the Mount Clark molars and other Cambrian SCFs. Among Orsten-type fossils, two isolated mandibles assigned to phosphatocopines from the middle Cambrian of Australia (Walossek et al. 1993, fig. 3A–D) have a finely divided mandibular gnathal edge with a narrow crescentic outline, unlike the Mount Clark molars. Among Cambrian macrofossils, specimens of Branchiocras cf. pretiosa from the middle Cambrian (Dru- mian) Marjum Formation of Utah (Aria & Caron 2017, extended data fig. 8) have perioral appendages with molar-like lineated regions. Equivalent structures are possibly present, but less well preserved, in the closely related Tokummia (Aria & Caron 2017, fig. 2d, f). Whether or not these structures are homologous to mandibular molars (see Discussion section), they lack the fringed margin seen in M. fimбриа. Contrasting toothed margins are observed on the perioral mouthparts of Waptia (Vannier et al. 2018, fig. 8) and fuxianhuiids (e.g. Yang et al. 2018, fig. 3f, g), whatever the limb identity; the putative mandibles of Ercaticunia, a small-bodied taxon imaged using micro-CT (Zhai et al. 2019a, fig. 2C), are too poorly preserved to show features of the gnathal edge.

Among extant mandibulates, a lineated scaly molar is well developed in various myriapods, basal hexapods, and branchiopod, malacostracan and remipede crustaceans (Edgecombe et al. 2003); a finely divided molar is also present in certain cephalocarid crustaceans (e.g. Carcupino et al. 2006) and ostracods (Richter & Kornicker 2006). Among these groups, the molars of branchiopods, especially anostracans, are most similar to the fossils: they commonly share a simple elongate D-shaped outline, a large number of scale rows increasing through ontogeny, a regular pattern of mostly unilateral length variation in the scales, and a field of differentiated spiny ornamentation extending obliquely along the dorsal margin from the posterior end (e.g. Ociosynska-Bankierowa 1933; Fryer 1983; Mura 1991, 1996; Tyson & Sullivan 1981; Mura & Del Caldo 1992, 1993; Peterson & Rosowski 1994; Davoodi et al. 2009; Hegna & Lazo-Wasem 2010). Individually these characters are not unique to anostracans because broadly comparable molars occur widely among branchiopods, including in spicicaudatans, cyclasteri- dans and cladocerans (Richter 2004), and in the Devonian Rhynie Chert branchiopod fossils Lepidocaris (Scourfield 1926; Fryer 1985) and Castracollis (Fayers & Trewin 2003).

The pattern of molar asymmetry in M. fimбриа provides an additional character for comparison. Among extant pancrus- taceans, asymmetric molar surfaces are characteristic of various branchiopods, eumalacostracans and lepismatic hexapods (Edgecombe et al. 2003; Richter 2004). The fossil molars resemble various branchiopods (including many anostracans) in having a strong ventral fringe on the right molar (e.g. Mura 1996), although the combination with a strong dorsal fringe on the left (Fig. 3) appears to be unique. The phylogenetic implications of the molar morphology in M. fimбриа are explored in the Discussion section below.

Because larger individuals have larger mandibles, the fossil molars can also be used to reconstruct the overall body size of M. fimбриа. Scaling relationships between molar length and body length imply a mature body length of at least 10 mm and perhaps more than 50 mm, depending on the comparative model (Harvey & Butterfield 2008, fig. S2). Using extant anostracan branchiopods as an analogue, which may be most appro- priate given the shared elongate proportions of their molars, the
650 μm length of the largest fossil molar translates to a body length of c. 40 mm. The smallest intact molars in the sample, at c. 190 μm long, correspond to body lengths of c. 10 mm, indicating a substantial ontogenetic range in the original population.

In extant taxa the molar processes of mandibles are invariably located immediately adjacent to the mouth opening, where they carry out the final stage of food processing prior to ingestion. The role of finely ornamented molar surfaces is to squeeze, scour and triturate any food particles trapped between them as they are rolled together in tight occlusion (Manton 1964). Where present, a setal fringe helps to restrict the escape of food particles, and assists their passage towards the mouth, whereupon they are ingested through pharyngeal swallowing movements (Fryer 1983). Where longer fringing setae are present, as in the Mount Clark molars, these can extend far into the oesophagus (e.g. Fryer 1965).

In general, the relative expression of biting and grinding surfaces on the mandibular gnathal edge is strongly influenced by its musculature and mode of articulation, which determine its range and style of movement (Snodgrass 1950; Manton 1964). The elongate shape and evenly distributed ornamentation of the Mount Clark molars imply that they were rolled together during the swing of the mandibles through a wide arc about an approximately vertical axis, as is the case in extant crustaceans and hexapods that have similar molar proportions (e.g. branchiopods, leptostracan malacostracans and, to a lesser extent, archaeognathans; see Manton 1964). Links between molar morphology and diet are not always clear in modern mandibulates. However, extensive and finely ornamented molar surfaces are generally associated with microphagy, at least within branchiopods and malacostracans, and extant anostracan species with similarly elongate and finely scaled molars that lack large marginal teeth have predominantly microphagous, suspension-feeding ecologies, as opposed to scraping or predatory habits (Mura 1995). The fine ornamentation of the Mount Clark molars would have allowed correspondingly fine food particles to have been handled with precision.

**Occurrence.** Lower Cambrian (Series 2; Stage 4) Mount Clark Formation, Northwest Territories, Canada, from drillcore Bele O-35 at a depth of 1351 m.

**Associated arthropodan SCFs**

Aside from the molar fragments, the Bele O-35 arthropod assemblage contains a rich diversity of cuticle fragments that may or may not belong to *Masticaris fimbriata* (*N* = 2811). Cuticle fragments with a more or less intact bounding shape, which have a reasonable chance of being identified as specific body parts, are described below in four categories: toothed blades, robustly spinescent elements, rectangular sheets, and paired triangles. Together these encompass c. 17% of specimens in the assemblage. Many of the remaining specimens (c. 63%) consist of spines and setae that are more or less disarticulated from the surrounding cuticle, and are preserved either singly or in groups (= arrays, or armatures). These are more challenging to categorize; however, repetitive associations and more intact arrays are classified into several informal categories with a focus on functionally distinct armatures and character-rich projection types (‘coplanar plumose armatures’ etc.) The remaining specimens in the assemblage, aside from the molars (c. 2%), consist of indeterminate arthropodan cuticle fragments (c. 18%).

In delimiting the categories, particular emphasis has been placed on the morphology of cuticular projections (setae, spines etc.), which are studied extensively in living crustaceans to give insights into phylogenetic and taxonomic relationships. As specialized mechanical, sensory and secretory structures, they also provide a unique view of localized functions (Garm & Watling 2013), especially those related to locomotion, grooming, reproduction, and above all, feeding. Much of the broader anatomical and behavioural context is lost in the disarticulated fossil material. However, the individual morphologies, collective arrangements and overall diversity of projections can carry detailed palaeoecological information.

The description of cuticular projections requires a specialist terminology, which we adapt from Garm & Watling (2013). This classification scheme was developed for modern crustaceans (especially the well-studied malacostracans) but is broadly applicable to fossil material. The definitions of spines and setae rely on cellular composition as well as external morphology. For example, setae are elongate projections with an approximately circular base and a continuous lumen containing sheath cells, whereas spines are simple, lumen-bearing projections that lack specialized cells and have a variety of cross-sectional shapes. In the fossil material a differentiation based on cellular composition is not possible, therefore we describe hollow projections as setae if they are slender, and as spines if they are comparatively robust, corresponding to a generic understanding of these terms. Solid projections of the cuticle, which can arise either from other projections or from the cuticle directly, are here termed setules (hair-like structures), denticles (tooth-like structures), and scales. We also utilize several widely used terms to describe the overall shapes of spines and setae, broadly corresponding to (but less restrictive than) the definitions of Garm & Watling (2013): simple projections typically lack ornamentation; serrate projections possess one or two distal rows (longitudinal series) of denticles; pappose projections have setules distributed either randomly, in whorls, or in multiple rows; and plumose projections have setules arranged in two rows. Compound terms (e.g. papposerrate, plumodenticulate) are available for projections with more complex morphologies. We do not distinguish cuspidate projections as a separate category of robust simple projections because there is likely to be a continuum in length : width ratio in our material.

Overall, we recognize 33 morphological categories of cuticular projections in the fossil assemblage, most of which are independent of size, and are intended to accommodate natural variability. For clarity and brevity in description we have labelled the different forms using a qualitative alphanumeric code (Table 1 and Fig. 4). Similar approaches are often used in the description of extant crustaceans (e.g. Coelho et al. 2000; Zimmer et al. 2009; Stuardo & Vega 2011; Keiler & Richter 2011). In our scheme the categories A, B, C and D refer to hollow projections (spines and/or setae) that can be broadly characterized as simple, serrate, pappose and plumose, respectively, whereas category E contains unusual
blunt-tipped forms, and category F contains solid setules, denticles and scales arising directly from the cuticle.

**Toothed blades**

*Figure 5*

**Material.** 87 specimens.

**Description.** Toothed blades are double-walled cuticle fragments with a tooth-like row of marginal spines (Fig. 5). They
vary in length from c. 100 to 800 μm and include forms that are ovoid, subtriangular or elongate in outline. The consistent marginal position of the spine row implies an original profile that was flattened and blade-like. The elements appear to lack a plane of bilateral symmetry, either perpendicular or parallel to the flat surface, suggesting that they were originally paired in life.

The tooth-like spination typically consists of a row of up to 12 longer spines, each up to 60 μm long and separated by a group of 1–9 smaller spines, each up to 10 μm long (Fig. 5). Typically the spiny margin is long and straight (Fig. 5A–D), although in some specimens it is gently curved (Fig. 5E) or sharply angled (Fig. 5M). The spines are mostly simple and without basal articulations, and have either sharp or blunt tips (= A1, A5 projections). They tend to increase in size towards the distal end of the spine row, which ends in a series of up to three spines that are conspicuously longer and more robust, and may be ornamented with a single row of denticles (= B1 projections; Fig. 5B–F). These distal-most spines articulate with the cuticle via basal sockets, which are most obvious where the spines have become detached (Fig. 5A), and are positioned so that their tips are more or less in alignment with others in the row (Fig. 5D).

The flat surfaces of the toothed blades often bear small, simple spines that insert into circles of thinner cuticle (Fig. 5C, E, I). Similar projections can occur in an irregular row along the non-toothed edge (Fig. 5I). In one specimen these spines are serrated rather than simple (= small B3 projections; Fig. 5A). In seven specimens the proximal part of the element bears a number of conspicuously long setae (e.g. 250–350 μm) that are variously simple or pappose in form (Fig. 5J, M, O).

Remarks. In their disarticulated condition, the toothed blades can be compared to a wide range of arthropodan body parts. However, a consideration of their morphological variability helps to rule out certain possibilities. For example, the specimens with more elongate outlines (e.g. Fig. 5J) resemble the tips of crustacean walking legs (e.g. Fryer 1960, text-fig. 1), but most have a substantially broader, rounded or triangular outline. The distinctive marginal spination recalls various arthropodan claws but the fossils lack the narrow pincer-like shape of comparable malacostracan and eurypterid claws (e.g. Rolfe & Dzik 2006; Van Roy & Ttetlie 2006), or the long terminal spine of subchelate claws (e.g. Petie & Muller 2007). In overall shape and marginal spination the fossils are more similar to the paired tail components of various crustaceans, including ostracods (e.g. Parker 1997), the Orsten stem-branchiopod *Rehbuchelia* (Walossek 1993), and certain shrimp-like forms (e.g. Mauchline 1980, fig. 5.4; Racheboeuf et al. 2000, fig. 8). However, all these structures lack the conspicuous long projections that attach proximally to some of the toothed blades, suggesting that the resemblance is superficial.

**FIG. 4.** Simplified schematic outlines of the various types of spines, setae and other cuticular projections in the Mount Clark SCF assemblage, labelled using the alphanumeric code described in the text and in Table 1.
Many Cambrian arthropods have blade-like spiny gnathobases on the proximal appendage parts, which can look strikingly like some of the toothed blades, including in overall outline, spine size gradation, and alternation of long and short spines (see examples from *Sidneyia* in Zacaï et al. 2016; Bicknell et al. 2018). In detail, the Mount Clark toothed blades have a particular pattern of spine alternation not matched elsewhere, and they lack the fibrous spine microstructure that seems widespread in both modern and Cambrian gnathobases (see Bicknell et al. 2018). Most importantly, however, there is a fundamental discrepancy in topology. Gnathobases have openings on either side of the spine row, both dorsally, where they attach to the body, and ventrally and/or laterally for the insertion of the walking limb (e.g. Bicknell et al. 2021, fig. 1; see also Nowak et al. 2018 for SCFs with convincing gnathobase characters). The Mount Clark toothed blades seem to have only one opening, suggesting that the spine row is developed distally on a limb or limb lobe rather than proximally on a limb base.

Two categories of potential modern analogues remain. One is the paired, food-handling crustacean mouthparts that operate by direct apposition, which, like the fossils, are characterized by a near-straight spine row with recurved, in-line terminal spines (Harvey & Butterfield 2008). In particular, the paired, opposing enditic lobes of various crustacean mouthparts have a comparably blade-like, subtriangular outline with a straight marginal spine-row, often with alternating spine lengths and longer terminal spines, and sometimes with longer setae inserted proximally. The roles of such structures, where known, are to grip, bite,

**FIG. 5.** 'Toothed blades' from the Mount Clark SCF assemblage. A, 34933, O35-TH-1-R12; image reflected. B, 142739, O35–6-S24. C, 34931, O35-TH-154-V15. D, 142740, O35-TH-148-Q17. E, 142741, O35-2-9-30-F23. F, 142742, O35-TH-109-D36; image reflected. G, 142743, O35–3-W18; image reflected. H, 108966, O35-2-9-15-K20. J, 34932, O35-2-9-28-O26; image reflected. J, 142744, O35-TH-125-G19. K, 142745, O35-2-9-40-P13. L, 142746, O35-TH-50-S30. M, 142747, O35–6-J24. N, 142748, O35–6-S43. O, 142749, O35-TH-20-G29. Scale bar represents 200 μm.
pierce, tear and otherwise manipulate larger food items (e.g. Hunt & Alexander 1991; Garm & Høeg 2001). Examples are found among the maxillules of cirripedes (e.g. Hunt & Alexander 1991; Høeg et al. 1994), the maxillules and maxillae of remipeds (e.g. Schram et al. 1986) and the mandibles, maxillules, maxillae and maxillipeds of eumalacostracans (e.g. Fryer 1960; Factor 1978; Lavalli & Factor 1992; Garm & Høeg 2000).

Overall, however, the best comparison is with the endopods (endopodites) of the thoracic limbs of branchiopod crustaceans, which in many taxa are modified for substrate scraping (Fryer 1985). Endopod outlines and armatures among living branchiopods are diverse, but broadly comparable examples are common among anostracans (e.g. Fryer 1966; Daborn 1979; Hegna & Lazo-Wasem 2010) and ‘conchostracans’ (e.g. Fryer & Boxshall 2009). Most significantly, the anterior trunk-limb endopods in Castracollis from the early Devonian Rhynie Chert (a possible stem-notostracan; Olesen 2009) are very close to some of the Mount Clark toothed blades in both outline and armature, and vary to a similar extent within individuals. They are also described as appearing more robust than the other appendage lobes (Fayers & Trewin 2003, figs 20B–C, 22A, 26B; p. 371), suggesting a higher preservation potential.

Individually, the toothed blades are no more similar to branchiopod endopods than they are to the oppositional mouthpart lobes of malacostracans and other crustaceans. However, their broad variation in outline, spination and setation suggests they were arranged in a series along the body, in common with branchiopod endopods, rather than being restricted to one or a few pairs of lobes among the mouthparts.

**Robustly spinose elements**

**Figures 6, 7**

**Material.** Around 60 specimens.

**Description.** Robustly spinose elements are characterized by a double-walled structure and heavy spination but are otherwise variable in shape and armature (Figs 6, 7). In general, the spination becomes more robust distally (i.e. towards the closed end, when preserved) and grades into armatures with more delicate spines and setae proximally (e.g. Figs 6A, B, D, I, F, 7A). The proximal part of the element is composed of thinner cuticle, and no basal articulations have been observed. Specimens with distinctive ‘hockey stick’ armatures are described separately (cf. Figs 15, 16).

In general, these armatures contain a high proportion of blunt or bulbous spines (e.g. A3, A4, A6, A7, A8), occasionally with pointed simple spines (= A5; Fig. 6L) or serrate spines with either one or two rows of serrations (= B1 or B2; Fig. 6H). Most specimens fall broadly into two possibly intergradational subcategories: those with comparatively short, often slightly recurved spines (Fig. 6H–K; see also Fig. 16L) and those with longer round-tipped spines oriented distally (e.g. Fig. 6D–G, M; see also

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**FIG. 6.** Robustly spinose elements from the Mount Clark SCF assemblage, including forms with marginal clubs (A, B, C); long-spine variants (D–G, M), and short-spine variants (H–L). A, 34939, O35–5-T29. B, 142750, O35–8-L36. C, 142751, O35–TH-80-S33. D, 142752, O35–TH-167-P52; image reflected. E, 142753, O35–TH-167-J17. F, 142754, O35–TH-143-R35. G, 142755, O35–NB-119-Q50. H, 135513, O35–TH-40-J22; image reflected. I, 142756, O35–TH-17-L40; image reflected. J, 142757, O35–NB-111-H43. K, 142758, O35–5-J17; image reflected. L, 34940, O35–TH-50-Q30; image reflected. M, 142759, O35–NB-120-M48. Scale bar represents 200 μm.
Fig. 7. A robustly spinose element from the Mount Clark SCF assemblage, in SEM view. A–B, 34946, O35-29-4; rectangle in A indicates area magnified in B to show details of C3 and C5 setae. Scale bars represent: 100 μm (A); 10 μm (B).

Fig. 16G). Notably divergent morphologies include a specimen with a particularly rounded outline and dispersed spination (Fig. 6L), and a rare ‘clubbed’ form (n = 2) with a marginal series of socketed, clavate spines (= A6, up to 80 μm long and 40 μm wide) set in ‘sockets’ (supra-cuticular articulations; Fig. 6A, B). Among the short-spine forms is a uniquely ‘paw-like’ specimen (Fig. 7) with a curved marginal row (or narrow field) of robust spines distally (= A3/A4; up to 70 × 30 μm) and grading to small, slender spines medially. This same specimen bears a proximal field of longer (100 μm) papposerrate setae, each of which has a wider basal portion with slender, sometimes bifurcating setules, and a distal portion bearing either a double row of minute bristles, producing a fuzzy appearance (= C3), or a single row of more robust serrations (= C5). Among the long-spine forms are several lobe-shaped specimens with armatures on two margins (Fig. 6F, G; see also Fig. 16G), and one specimen (Fig. 6M) consisting of three articulated lobes, decreasing in size distally, all with robust armatures at their tips and more slender, basally pappose setae proximally (cf. C3).

Remarks. The robustly spinose elements are likely to represent lobes of appendages that functioned in the heavy-duty processing of food, or in its acquisition from a substrate. In many arthropods such lobes are limited to the mouthparts, although in branchiopods in particular, they may extend along the body as the endites of a series of thoracic appendages. The specimen with three articulated lobes (Fig. 6M) confirms that at least some of the elements with long-spine armatures occurred as elongate endites, repeated along a limb with more or less variation in ornamentation. Many of the elements with short-spine armatures (e.g. Figs 6I–K, 7) conform to the same general organization, with robust and slightly recurved spination distally, grading to more slender spines and setae proximally. Often these setae express a distinctive motif of having thin walls and long setules at the base, contrasting with a robust tip of some sort (e.g. Figs 6F, I, M, 7B; see also the hockey-stick armatures, below). As such, most of the long-spine and short-spine specimens among the robustly armoured elements are plausibly compared with one another in spite of their diversity, and interpreted as endites that varied along a limb and probably also along the body.

In general, appendage lobes and articles with spiny armatures are widespread among arthropods, including Cambrian forms, with examples known from both Orsten-type assemblages (e.g. Maas et al. 2003) and the Burgess Shale (e.g. the spiny mandibular palp articles of Waptia; see Vannier et al. 2018, fig. 8c, d). However, the extent and range of adaptations in the Mount Clark sample is more suggestive of the along-body and along-limb variation in branchiopod endites; for example, see Fryer (1988) for notostracans, Fayers & Trewhin (2003) for the Rhynie Chert Castacollis, and especially Fryer & Boxshall (2009, fig. 8) for a laevicaudatan conchostracan, noting the armature distribution from medially recurved robust spines distally on endites, versus gracile setae on their proximal flanks.

The prevalence of club-shaped spines in the Mount Clark assemblage is notable, given that comparable forms are rarely reported among modern crustaceans. The short clubs in a marginal series in two specimens (Fig. 6A, B) are particularly distinctive. Spines with similar shapes (although not arrangements) occur on the subterminal articles of walking legs in certain extant decapods (e.g. Berggren 1990, fig. 2) and isopods (e.g. Riseman & Brusca 2002, fig. 30) although their function has not been discussed. Those in the Mount Clark assemblage seem to represent particularly robust variants of food-handling armatures.

Rectangular sheets
Figure 8

Material. Large rectangles: 10 specimens. Small rectangles: more than 229 specimens.

Description. Large rectangles measure up to 800 μm long and 600 μm wide, and possess a longitudinal line of symmetry that is expressed through varying cuticle opacity and the distribution of small-scale pockmarks (Fig. 8A–E). The bounding edges tend to be irregular, and cuticular projections are generally lacking, although one comparatively small specimen (Fig. 8D; 540 × 390 μm) has well-preserved longitudinal edges that bear long (c. 150 μm) pappose setae armed with slender setules proximally and fine denticles at their tips (= C6). Two sheet-like...
specimens with divergent morphologies include a large (c. 1.5 mm) specimen (Fig. 8F) with a 'rippled' surface texture and a marginal ornamentation of simple, narrow-tipped spines (= A2; Fig. 8G).

Another specimen is notably large (840 µm × 240 µm) and thick-walled (Fig. 8H), with longitudinal lineations and a well-defined crease that extends part-way along the midline (Fig. 8I).

**FIG. 8.** Rectangular sheets and related elements from the Mount Clark SCF assemblage, including large rectangles (A–E), other large cuticular sheets (F–I), small rectangles (J–P) and other setulose cuticular sheets (Q–S). A, 142760, O35-TH-169-R19. B, 142761, O35-1-S30. C, 142762, O35-TH-169-U14. D, 142763, O35-TH-162-N35. E, 142764, O35-TH-142-S36. F–G, 142765, O35-TH-153-Q19; rectangle in F indicates area magnified in G to show marginal A2 spines. H–I, 142766, SEM-O35-40-1; rectangle in H indicates area magnified in I to show longitudinal fabric in high-intensity transmitted light. J, 142767, O35-TH-40-L13. K, 142768, O35-TH-32-H31. L, 142769, O35-TH-134-P8. M, 142770, O35-TH-154-N17. N, 142771, O35-2-9-14-Q20. O, 142772, O35-TH-139-T30. P, 142773, O35-2-9-13-S11. Q, 142774, O35-TH-157-H41. R–S, 142775, O35-TH-103-N13; rectangle in R indicates area magnified in S to show F2 and F3 setules or denticles. Scale bar represents: 300 µm (A–G, E); 250 µm (D); 460 µm (F); 120 µm (G, J–N, P, R); 200 µm (H); 70 µm (I); 220 µm (O, Q); 40 µm (S).
In contrast, small rectangles (n > 229) have a characteristic warty ornamentation and rather smaller dimensions (160–330 μm long and 80–200 μm wide; Fig. 8J–P). Some specimens preserve thin-walled lateral extensions bearing elongate fields of papoose setae (= C19) that are short (40–80 μm), slender and densely set (Fig. 8M). The original articulated configuration is seen in specimens in which up to three elements are joined end to end, with flattened outlines that suggest a more strongly three-dimensional (broadly U-shaped) profile in life (Fig. 8N–P). Many specimens are partially folded or enrolled (e.g. Fig. 8L).

A unique specimen consists of two imbricating sheets (Fig. 8R): the overlying sheet is similar in size, shape and texture to a typical small rectangle, but the underlying sheet is folded beneath itself distally (apparently as an original feature) and bears a symmetrical arrangement of small (<20 μm) unbranched or serrate projections (= F2, F3) and a fine-scale (1–3 μm) reticulate ornamentation on its upper surface (Fig. 8S). The underfolded surface has a medial band of setules (= F1). A somewhat similar specimen (Fig. 8Q) consists of a single folded sheet with a bilaterally symmetrical arrangement of setules.

**Remarks.** A general assumption can be made that any bilaterally symmetrical elements in the assemblage were positioned along the midline of the body. In support of this, both the large and small rectangles tend to be composed of relatively thick cuticle, and often bear microstructures (warts, polygons) that are typical of external midline sclerites such as tergites, sternites and carapaces. Most informatively, the end-to-end fusion of the small rectangles suggests that they are sternites rather than tergites, which tend to be imbricated. Furthermore, the ‘pinched’ pattern of ornamentation on some specimens (e.g. Fig. 8J, K) suggests an hourglass shape that is widespread among Cambrian arthropod sternites (e.g. Budd 2021, fig. 4f; Aria & Caron 2017, extended data fig. 7c). The fine fringes of setae in some small rectangles (e.g. Fig. 8M–P) are consistent with a sternite interpretation, and suggest a role in channelling food particles.

The large rectangles offer fewer constraints in their interpretation, but they could be tergites, or perhaps sternites from larger individuals; sternites with robust marginal setation (as in Fig. 8D) are not unknown among modern crustaceans (see Thomas 1970, fig. 24a). The identities of other sheet-like elements are more obscure. In its overall shape and converging fields of setae, the fossil with two imbricating sclerites (Fig. 8R) resembles the labrum (‘upper lip’) of certain crustaceans (e.g. Koeman et al. 2008, fig. 2D), although no additional diagnostic characters are evident. The two very large specimens (Fig. 8F, H) conceivably represent parts of a carapace or headshield.

**Paired triangles**

**Figure 9**

**Material.** 14 characteristic specimens, plus 22 partly similar specimens.

**Description.** Paired triangles are single-walled, bilaterally symmetrical elements characterized by a medial region of thicker cuticle in the form of paired triangles (e.g. Fig. 9B) or an undivided rhomboidal sheet (e.g. Fig. 9I). The long and short axes of the paired triangles, or equivalent rhomboids, range from c. 70 μm to 360 μm and from 40 μm to 190 μm, respectively. Evidence for homology of these various elements comes from a shared ‘apical’ morphology: the more acute points of the triangles, which tend to be particularly thick-walled, extend into a narrow longitudinal strip of thin-walled, fringed cuticle (e.g. Fig. 9C, H). The fringes are a continuation of setal rows that attach to the outer margins of the triangles (Fig. 9B, D, K), although these are seldom preserved. Basally the triangles merge with a broad expanse of thin cuticle bearing very fine papoose setae (= C8), c. 70 μm long, that are directed obliquely within two symmetrical fields in a medial and apical direction (Fig. 9A, B, E, F). The overall structure is rhomboidal, and is similar in its proportions to the paired-triangle region enclosed within it (Fig. 9B).

Taking into account the variable direction of flattening, the triangles are reconstructed as a pair of robust cuticular ridges that taper and converge apically. In most specimens the medial region is smooth, although one large rhomboidal specimen has a symmetrical ornamentation of warts and lineations (Fig. 9I). The fringes on the lateral margins are composed of apically directed simple setae (= A12) up to 40 μm in length. In some specimens the fringing setae have minute club-shaped or globular tips (= A13; Fig. 9H). Where the fringes extend beyond the apices of the triangles along the narrow cuticular strip, the fringing setae are paralleled by unusual, short projections that appear to originate as fine-scale divisions of the cuticular sheet (Fig. 9C, H, O).

**Remarks.** Like the rectangular sheets, the paired triangles are assumed to have occupied a midline position on the body. Butterfield (1994) compared them to the crustacean labrum, which is a lobate projection that arises immediately anterior to the mouth and forms the ‘upper lip’ of the oral chamber. Although certain crustaceans do possess a labrum with a paired triangular outline and fringing setae (e.g. the ostracod _Vargula_ figured in Vannier et al. 2018, fig. S9), the fossils are single-walled sheets rather than double-walled lobes, and unlike any labrum are confluent apically with a strip of cuticle that extends away in the same plane. This last property also suggests that they cannot represent a structure such as the ‘median triangular sclerite’ that projects from between the eyes in _Waptia_ (Vannier et al. 2018, fig. 4); instead they must be flanked by other structures both to the front and behind.

The paired triangles are more comparable to the sternum in modern crustaceans and certain fossil taxa. This ventral region of the body wall is situated immediately posterior to the mouth and is formed from a series of more or less fused sternites. It is typically bordered by fields of cuticular projections, forming a continuation of the food groove where present. The projections tend to be directed orally (e.g. Hoffmeyer & Prado Figuerola 1997; Tziouveli et al. 2011, fig. 3), consistent with a role in directing food towards and into the mouth. In particular, the thick-walled, originally three-dimensional triangular regions in the fossils are comparable to paragnaths, which are inflated, paired or fused outgrowths of the crustacean sternum; they form
Fig. 9. Mirrored triangle elements from the Mount Clark SCF assemblage. A, 142776, O35-TH-160-D32. B–C, 109201, O35-2-9-39-K22; rectangle in B indicates area magnified in C to show apical ornamentation. D, 142777, O35-2-9-21-U18. E, 142778, O35-2-9-33-U37. F, 142779, O35-TH-161-U20. G–H, 142780, O35-TH-2-L36; rectangle in G indicates area magnified in H to show fringed apical strip. I, 109200, O35-2-9-31-P25. J, 142781, O35-TH-131-Y38. K, 142782, O35-2-9-44-N23. L, 142783, O35-TH-41-G26. M, 142784, O35-TH-149-P34. N, 142785, O35-2-9-23-U32; image reflected. O, 142786, O35-TH-127-H12. P, 142787, O35-2-9-26-N37. Scale bar represents: 100 μm (A, B, D–G, I–P); 55 μm (C); 50 μm (H).
the labium (‘lower lips’) of the oral region (see Wolff & Scholtz 2006). In this interpretation, the fields of delicate setae would have been located posteriorly, on or behind the paragnaths, and the strip of cuticle with fringes would have extended anteriorly, towards (and perhaps into) the oesophagus. Among extant crustaceans, notostracan branchiopods provide a close model for comparison, especially in having parallel comb-like fringes (the ‘mandible cleaning rakes’) extending orally from the paragnaths (see Cannon 1933a, fig. 24; Fryer 1988, p. 69, fig. 102). Among fossils, the stem-branchiopod *Rebbachisella* exhibits a sternal region, complete with paragnaths, that is similar in outline to the Mount Clark paired triangles (Walossek 1993, pl. 27:4).

**Coplanar plumose armatures**

*Figures 10–12*

**Material.** 106 specimens.

**Description.** Coplanar plumose armatures contain a series of up to 40 plumose setae aligned in a single plane, often with diverse superimposed arrays of accessory setae (Figs 10–12). The plumose setae bear straight, slender setules that are paired in a strictly opposite arrangement and are inserted at regular, extremely narrow intervals, typically 1 µm or less (≥ D1–D4), defining a mesh with micron- or sub-micron-scale openings (e.g. Figs 10B, 11A). Depending on the number and length of setae, which range from 85 µm to 600 µm, the surface area of more complete armatures measures between c. 0.01 mm² and 0.26 mm².

The types and arrangements of accessory setae are diverse. To summarize, the plumose setae can grade laterally into plumodenticulate (≥ C10) and/or pappose (≥ C9) setae, and may be paralleled by rows of bulky pappose, short plumose (≥ D4), short pappose (≥ C8) and robust papposerrate (≥ B6) setae. Occasionally the armature is preserved on the remnants of an appendage lobe, which locally bears small setules (≈ F1) that arise directly from the cuticle.

The most extensively preserved specimen (Fig. 10A) contains a series of 34 plumose setae (≥ D1), each up to 300 µm long (Fig. 10B). The overall armature has an arcuate distal outline, with the longest setae towards the middle of the series. An underlying and mostly obscured series of plumose setae, at right angles to the first, may have formed part of the same armature, or represent the superposition of two adjacent armatures (Fig. 10C). The unobscured series is paralleled by a row of 12 sturdy papposerrate setae (≥ B6), each up to 130 µm long, which bear long, randomly inserting setules in their middle portion, fine biserial serrations distally, and terminal pores (Fig. 10G–J). Contrasting, notably delicate pappose setae (≥ C8), only 1–2 µm in diameter, arise from among the bases of the plumose and papposerrate setae (Fig. 10D). Two further setal types, both of which are slender in outline and more than 100 µm long, are preserved in outlying positions: a pappose form (≥ C9) has uniform, filiform setules that are sparse towards the base but which are more densely arranged distally (Fig. 10K); a highly distinctive plumodenticulate form (≥ C10) bears minute (c. 1.5 µm) scale-like setules distally and exceptionally long (c. 30 µm) setules proximally, the latter arising from more or less opposite insertion points at intervals of c. 2 µm (Fig. 10E, L, M).

The largest coplanar plumose specimen (Fig. 11B, C) has a series of more than 40 plumose setae, each up to 600 µm long, paralleled by a series of much smaller (c. 90 µm) plumose setae (≥ D4), plus a series of small pappose setae (≥ C8), and a series of six long and robust pappose setae (≥ C9) that are partly obscured by adherent material. A similar setal association is preserved in a medium-sized specimen imaged using SEM (Fig. 12A, B), which has a series of c. 28 plumose setae (≥ D1), each up to 250 µm long, paralleled by a similar number of much smaller plumose setae (≥ D4) only 60–90 µm long (Fig. 12B), plus a series of long pappose setae (≥ C8) and a group of at least three robust pappose setae.

A small but intricate specimen with a substantial area of attached cuticle (Fig. 11D–F) has a series of at least 12 plumose setae (≥ D1), each up to 85 µm long, extending into a series of 20 plumo-pappose setae (≥ C7) with unusual, strongly recurved setules proximally, and densely packed, filiform setules distally (Fig. 11F). A further five setae, partly detached, include plumodenticulate forms (≥ C10; Fig. 11D). The principal series is paralleled by very small setae (c. 10 µm long, the fine structure of which has not been resolved. A third parallel series contains robust papposerrate setae (≥ B6) with an unornamented bulbous base, a cluster of long setules medio-distally, and a flattened tip with biserial serrations (Fig. 10E). These grade into more slender variants (possibly C9 and/or C10) that are aligned in a series that diverges from the principal plane, implying a degree of three-dimensionality to the original armature.

Several of the more fragmentary specimens have additional fine-scale variations in setal morphology (Fig. 12C–P). In contrast to the typical plumose setae, which have rounded, feather-like tips (≥ D1; Fig. 12F), some specimens have an unornamented distal-most shaft (≥ D2; Fig. 12G), or a distal tuft of recurved, claw-like setules (≥ D3; Fig. 12H–K). Some plumose setae have a series of spur-like projections, either smooth or setulized, along their ‘posterior’ edge (Fig. 12F, L–O). Among specimens with accessory setal types, one has a variant of the unusual plumodenticulate form (≥ C10) in which the exceptionally long setules are more strictly paired and more widely spaced (Fig. 12P), while another contains a bizarre setal type (≥ E1) that is distinguished by a distal cluster of expanding hook-like setules (Fig. 12C, D).

**Remarks.** Setal armatures comparable to the coplanar plumose specimens are widespread among extant crustaceans, where they are used in the precise handling of fine particulate food. The coplanar arrangement of the type D1–3 projections, combined with the close spacing of their setules (typically 1–2 µm) in opposite series less than 180° apart, identify them as filter setae (Cannon 1933a, p. 274; Dennell 1934, p. 140). The overall proportions and curved distal outlines of the arrays allow them to be described as filter plates (e.g. Manton 1977, p. 157). At a finer scale, equivalents of the Mount Clark filtering setae with recurved tips (≥ D3) occur in *Nebalia*, where they link together the filter plates of adjacent appendages (Cannon 1927), whereas variants of filter setae with naked tips (cf. D2 setae) have been
described from cladocerans (Cannon 1933a, fig. 21b), and those with spurs are known from both anostracans (Cottarelli et al. 2007, fig. 6f) and cladocerans (cf. ‘brush spinules’ in Fryer 1963, p. 354). In contrast, other types of arthropodan plumose setae tend to be more sparsely setose and more widely spaced (cf. Mount Clark D5 setae, described below). These coarse plumose setae typically function as screens (e.g. for limiting particle loss from a feeding chamber; Fryer & Boxshall 2009) and fringes (e.g. for increasing the surface area of paddles, such as swimming legs and tails; Hessler 1985).

Among crustaceans, filter plates occupy various non-homologous body positions and are therefore convergent to some extent (Dennell 1933; Manton 1977; Martin & Christiansen 1995). In terms of size, setal count and overall shape, the fossils most closely resemble the filter plates on the thoracic appendage lobes of various branchiopods (anostracans, cladocerans and a spinicaudatan; Cannon 1933a), the mandibles and/or maxillules of some ostracods (e.g. Cannon 1933b; Horne et al. 2011) and the maxillae of various eumalacostracans (especially those of mysids and syncarids; Cannon & Manton 1927, 1929; less so those of amphipods, cumaceans and tanaidaceans; see Marshall & Orr 1960). In contrast, the filtering devices on the thoracic legs of both Nebalia (a leptostracan malacostracan) and euphausiid eucarids are less similar overall, being constructed from more linear arrangements of less finely or precisely meshed setae (Cannon 1927; Hamner 1988). Other crustacean filters that differ substantially from the fossils in setal spacing or overall shape include the cirral filters of cirripedes (Hunt & Alexander 1991), the maxillary filtering baskets of copepods (Marshall & Orr 1960, fig. 1a), the diverse non-maxillary filter screens of amphipods and decapods (Marshall & Orr 1960; Graham 1983), and the internal (foregut) filters of various malacostracans (e.g. Watling 2013, fig. 8.5).
The diversity and arrangement of attached accessory setae in the Mount Clark filters is likely to reflect the general requirement for particles, once captured, to be scraped from the setal screen by mechanical processes (Cannon & Manton 1929; Marshall & Orr 1960). For example, the serial thoracic filter plates in branchiopods, Nebalia and euphausiids clean those on neighbouring limbs by way of filter-parallel rows of contrasting setal types (Cannon 1927, 1933a; Hamner 1988). Equivalent mechanisms are developed in the singular maxillary filters of eumalacostracans (Cannon & Manton 1927, 1929). Filter-parallel series of stout, serrated setae (cf. Mount Clark type B6) are known in various branchiopods (Cannon 1933a, figs 2 and 22; Williams 2007, fig. 5A), maxillary-filter-bearing eumalacostracans (Cannon & Manton 1929, p. 179 and text-fig. 2b; Cannon & Manton 1927, plate 3 fig. 2b), and euphausiids (Hamner 1988); these are often referred to as cleaning- or comb-setae. Similarly, filter-parallel series of much smaller, usually simple projections have been documented in various branchiopods (Cannon 1933a; Williams 2007) and Nebalia, which also has filter-parallel rows of short plumose setae and very long pappose setae (Cannon 1927, text-fig. 4), equivalent to the Mount Clark D4 and unclassified pappose forms, respectively.

These various similarities with extant crustaceans reinforce the functional interpretation of the Mount Clark filter plates without suggesting a clear phylogenetic pattern. However, important comparative material from the middle Cambrian Earlie Formation (Ceepee Reward assemblage) of Saskatchewan (Harvey et al. 2012) includes more fully articulated specimens with filter plates borne on much larger appendages. At least in this marginally younger material (Mioalginian Series), the setal armatures grade into appendages with a more robust setation and a series of protruberant lobes, presumably representing endites (Harvey et al. 2012, figs 3, 54). Among extant crustaceans, the presence of arcuate-outlined filter plates on extensive lobose appendages is shared only with the phyllopodous thoracic filters of branchiopods.

Among other fossil branchiopods, thoracic series of comparable, coplanar filter plates are known from the Devonian Rhynie Chert Lepidocaris (Scourfield 1926; Fryer 1985) and probably also Castracollis (see the ‘meshing spines’ of Fayers & Trewin 2003), in keeping with their branchiopodan affinities. Walossek (1993, p.100) compared the enditic thoracic armatures of late Cambrian Rehbachiella to the filtering devices of branchiopods, in particular, to which they were proposed to be homologous (see Olsen 2009). However, there is no obvious similarity between the Mount Clark and Rehbachiella structures: in Rehbachiella the putative filtering setae are arranged in multiple small arcs rather than long coplanar series, and have a substantially larger (c. 2 mm) inter-setule distance (Walossek 1993, p. 57).

In extant crustaceans, filtering (i.e. the ‘separation of particles from fluids by use of porous media’; Rubenstein & Koehl 1977, p. 981) is achieved either by sieving, or by a more indirect process of particle concentration (e.g. Koehl & Strickler 1981). There are a number of mechanisms by which particles smaller than the mesh size can be captured, at least in theory (e.g. Rubenstein & Koehl 1977). Nevertheless, mesh size is an adequate predictor of particle retention efficiency in living crustaceans (e.g. Brendelberger 1991), and extant taxa with inter-setule distances of c. 1 mm are able to efficiently handle particles ranging down to the size of bacterial cells (Geller & Müller 1981; Barnett et al. 2007). Clearly, the micron or submicron scale of the Mount Clark filtering mesh would have allowed the precise capture and manipulation of very fine particles.

Filter plates are not used exclusively in suspension feeding (i.e. the gathering of food particles suspended in surrounding water) and ‘filter feeders’ in a more general sense can have diverse ecologies (Marshall & Orr 1960). The maxillary filters of various detritivorous eumalacostracans, for example, manipulate particles that have been generated through the scraping of a substrate (Cannon & Manton 1929). Even so, filter plates are invariably associated with suspension feeding in branchiopods, leptostracans and euphausiids, all of which have repeated sets of filter plates on successive trunk appendages. Such features do not necessarily imply a pelagic habit, however: although euphausiids and some anostracans swim in open water (Hamner 1988; Mura 1995), many other anostracans are nektobenthic (Mura 1995), and some cladocerans filter within burrows (Fryer 1968). On balance, it is reasonable to assume that the Mount Clark filter plates were used at least some of the time in suspension feeding, in a planktic and/or nektobenthic setting.

Arrays of saw-toothed and distally bifurcate setae
Figures 13, 14

Material. 7 extensive setal fields, plus isolated individual projections.

Description. Saw-toothed setae (= C14) have a shaft of mostly uniform width with one bluntly serrated edge (Figs 13B, H,
FIG. 13. Bifurcate and saw-toothed setae from the Mount Clark SCF assemblage. A–B, 34929, O35-2-9-23-R19; rectangle in A indicates area magnified in B to show details of the saw-toothed (C14) setae. C, 142799, O35-TH-16-O29, D, 142800, O35-2-9-9-O39. E, 142801, O35-TH-103-R16. F, 142802, O35-TH-53-E22. G–H, 34942, O35-2-9-5-S17; rectangle in G indicates area magnified in H to show the saw-toothed (C14) setae; image in G cropped to fit (displaced setae extend from top of specimen). I–K, 142803, O35-TH-135-W37; rectangles in I indicate areas magnified in J and K to show saw-toothed (C14) setae and a gradational variant, bifurcate (C16) setae, respectively. Scale bar represents: 75 μm (A, G, I); 40 μm (B, H, J, K); 100 μm (C, D, F); 200 μm (E).
Long setules may also be present, inserting in two rows on either side of the serrations (Fig. 14F, G). A distal bifurcation is often developed, with one branch continuing the saw-toothed ornament and the other, typically longer branch bearing a distal tuft of setules (Fig. 13B). A variant form has distal setules but no bifurcation (Fig. 13F). In one particularly extensive array of more than 100 individual setae (Fig. 13I–K), typical saw-toothed setae grade into longer setae that lack a saw-toothed edge, but exhibit a conspicuous distal bifurcation with two pappose branches of unequal length (= C16 setae). Comparable distally bifurcate setae also occur in the assemblage as individuals or small groups (n = c. 20; Figs 13C–E, 14A–C). These lack saw-tooth serrations and have two branches of subequal length and width, and contrasting ornamentations (= C15 setae). Typically the undivided shaft is pappose, with setules more closely spaced distally (Fig. 13C, D), and then distal to the branch point the narrower and longer branch bears densely set setules, while the stouter branch bears a fringe of fine serrations at its tip (Fig. 14C). Overall, the length of the bifurcate setae (c. 90–300 μm) exceeds that of the saw-toothed setae (c. 60–180 μm).

Remarks. A surprising but strikingly detailed modern analogue for the arrays of saw-toothed and bifurcate setae is provided by the substrate-scraping cheliped (pereiopod) claws of atyid decapods (Fryer 1960, 1977; Felgenhauer & Abele 1983). In Caridina these include setal morphologies that are precisely equivalent to the C14–C16 Mount Clark setae in having blunt serrations and distal bifurcations with longer pappose and shorter serrate branches, and in grading into non-serrate pappose forms (Fryer 1960). The claws of Caridina obtain particles by raking the substrate using a grasping motion in which, because of tiering within the armature, stouter serrate ‘comb spines’ are first to pass over the substrate, followed by the intermediate ‘brush and comb setae’, and finally the long, non-toothed pappose ‘brush setae’, releasing and gathering successively smaller particles (Fryer 1960).

Although the Mount Clark setae would have been well suited to an analogous role, the fossils from the middle Cambrian Earlie Formation (Ceepee Reward assemblage) (Harvey et al. 2012, figs S3, S4) suggest a contrasting anatomical and phylogenetic context: the saw-tooth setae occur alongside arcuate filter plates and other setal armatures on larger, lobate structures that are interpreted as the thoracic limbs of a total-group branchiopod. Viewed in this context, the fossil saw-toothed setae are recognized as entirely convergent on those of atyid decapods. The Mount Clark specimens, although disarticulated, are likely to have been borne on Earlie-type appendages, supported by their
matching morphologies and co-occurrence with near-identical filter plates.

In various extant branchiopods, robust scraping armatures are borne in distal positions on the thoracic limbs and are used in substrate-scraping roles (e.g. Daborn 1979; Fryer 1985). However, the comparatively small size of the saw-toothed setae relative to contiguous armatures in the middle Cambrian specimens (Harvey et al. 2012, fig. S3) suggests a different role, conceivably in cleaning the filter plates, other parts of adjacent appendages, or the food groove more generally. Comparable roles have been considered for the various accessory setae that occur within the Mount Clark coplanar plumose armatures (see above).

Hockey-stick armatures
Figures 15, 16

Material. 9 specimens.

Description. Hockey-stick armatures consist of diverse spines and setae arranged in a strongly linear array. The diagnostic character is a row of simple, distally recurved setae (‘hockey sticks’, = A9; Fig. 15B, D) that grade into more robust forms, often with straight shafts and one or two rows of blunt serrations (= B7; Figs 15A, 16N, O) or robust, angular tips (= A10; Fig. 15C). Associated setal morphologies include forms with finely serrated distal tips (= C4; Fig. 15B, below), and slender variants with minute bilateral serrations (‘fuzzy’ setae; = C3; Fig. 16M). The hockey-stick setae and associated forms tend to be thinner-walled at the base and more heavily cuticularized at the tips, and often have fine setules, sometimes branched, inserted proximally on the shaft in characteristic half-rings or clusters (Figs 15B, 16B, C, K); these properties are shared with setae positioned proximally on many of the robustly spinose elements (cf. Figs 6F, M, 7B).

In the most intact specimens the armature is arranged in a line or narrow field along the margin of a lobate cuticle fragment, with the recurved tips of the hockey-stick setae oriented in a common direction (Figs 15A, C, 16G). One specimen (Fig. 16G–K) has a second, partly superimposed lobe or sublobe with a more robust armature that grades between low rounded humps proximally (= A3) and elongate clubs distally (= A8), which on its own would be classed as a robustly spinose element (long-spine variant). Similarly, a specimen with the characteristic ornament of a short-spine robustly spinose element (Fig. 16L–O) also contains setae approaching a hockey-stick form, along with the fuzzy setae and distally serrate setae.

Remarks. The hockey-stick armatures represent a highly distinctive variant of the long-spined, blunt-tipped armatures noted on some of the robustly spinose elements. Articulated specimens (Figs 15A, 16G, L) confirm that the hockey-stick armatures were borne on lobes (presumably endites) contiguous with robustly spinose elements. The proportions and spatial arrangement of the hockey-stick setae and associated fuzzy and serrate setae imply a role in scraping. Broadly similar arrays are known from the scraping mouthparts of various crustaceans and aquatic hexapods, including the scraping armatures located along the margins of the distal endites in many branchiopod crustaceans. These range from short series of slender or stout serrated projections in cladocerans and anostracans (e.g. Fryer 1963, text-fig. 25; Fryer 1985; Hegna & Lazo-Wasem 2010) to the densely populated fields of slender to robust, often hook-like scrapers in a laevicaudatan conchostracan (Fryer & Boxshall 2009). The latter has elongate endites that are especially reminiscent of the Mount Clark specimens in having the longest and most robust projections situated distally (cf. Fig. 16G, L), and hooks facing in the opposite direction (cf. Fig. 15A, C); that is, medio-proximally, or into the feeding chamber. Notably, the notostracan Strudops from late Devonian non-marine deposits of Belgium preserves arrays of robust-tipped hockey-stick setae on its thoracic limbs (Gueriau et al. 2016, fig. 4), proving a long history of comparable armatures in branchiopod crustaceans. Together, the robustly
spinose elements, including those incorporating hockey-stick armatures, would have been well suited to a role in the heavy-duty processing of a substrate and the precise transfer of particles towards a food groove.

**Arrays of pappose setae with long and short setules**

*Figure 17*

**Material.** At least six arrays among more than 300 groups of mostly uncategorized pappose setae.

**Description.** Some categories of pappose setae are notable for having both long and short setules in their proximal part (= C11–C13). These setae measure up to several hundred microns long and occur in arrays of up to several tens of setae. The proximal setulation typically consists of longer setules arranged in opposite pairs at 5–10 μm intervals, with shorter and more densely packed setules lying in-between (e.g. Fig. 17B, J, L). Depending on the direction of flattening, the shorter setules are not always visible. The distal setulation is variable: some setae have brush-like tips (= C11; Fig. 17H, M) whereas others have a finely serrated appearance, either with a narrow, tapering outline.
**Fig. 17.** Arrays of pappose setae with long and short setules from the Mount Clark SCF assemblage. A–C, 34945, O35-28-5; rectangles in A indicate areas magnified in B and C to show shafts and tips, respectively, of C12 and C13 setae. D–G, 142810, O35-43-3, a poorly articulated array; rectangles in D indicate areas magnified in E–G to show the C12 setae (E) and the accessory robust, finely serrate (B5) setae (F, G). H, 142811, O35-29-3, a group of C11 setae. I–J, 142812, O35-44-6; rectangle in I indicates are magnified in J to show setulation. K–L, 142813, O35-41-8; rectangle in K indicates area magnified in L to show setulation. M, 142814, O35-19-6; detail of C11 setae with densely arranged setules distally. Scale bars represent: 100 μm (A); 5 μm (B, C, F, G, J, L); 50 μm (D, H, K); 10 μm (E, M); 20 μm (I).

(= C12; Fig. 17C, E) or a broader, biserially setulated morphology (= C13; Fig. 17C). These variants may co-occur within a single array (Fig. 17A). One array incorporates a pair of more robust, serrated knife-like setae (= B5; Fig. 17D–G).

**Remarks.** Pappose setae with long and short setules have been observed in aquatic insect larvae, where they are considered to be characteristic of feeding by passive filtration (Palmer 1998). The Mount Clark specimens may well derive from the same appendages as the filter plates, although no direct associations have been observed.

**Arrays of compound pappose setae**

**Material.** Two isolated setal arrays.

**Description.** Pappose setae that bifurcate one or more times along their length have been observed in two setal arrays, where they measure up to 90 μm and 150 μm, respectively. Often the side branches truncate after a short distance (= C17; Fig. 18C) or at the bifurcation point itself (= C18; 18G, H). As a result of successive bifurcations, the width of the setal shaft decreases incrementally along its length. Distally, the setules are densely set and inserted randomly (Fig. 18D, F), whereas proximally they are inserted at greater intervals, along only one side of the shaft (Fig. 18H).

**Remarks.** The compound pappose setae are highly distinctive; we have not encountered comparable forms in published descriptions of extant arthropods. The dense arrangements of the Mount Clark setae and their setules would suit them to a role in a setal screen.

**Arrays with bulb-tipped setae**

**Figure 19**

**Material.** Setal arrays borne on three cuticle fragments.

**Description.** Arrays with bulb-tipped setae occur on lobe-shaped cuticle fragments. They are defined by the presence of bulb-tipped setae (= A11), which have a simple, gradually tapering shaft and a distinctive bulbous tip, probably with a terminal pore, and sometimes with a sub-apical setule or tuft of setules (Fig. 19B, F, G, J–L). The best preserved specimen (Fig. 19A–H) consists of a rounded cuticular lobe with a cluster of at least 11 bulb-tipped setae, each 20–170 μm in length and bracketed by two clusters of coarsely plumose setae (= D5) in which the setules are spaced c. 5 μm apart (Fig. 19E). At the opposite end of the lobe are three robust spines up to 250 μm long with distal knife-like serrations (= B5; Fig. 19C, H). The surface of the lobe is ornamented in places by setules (= F1) up to 15 μm long (Fig. 19D). A similar overall arrangement is seen in a second specimen, in which a cluster of around seven bulb-tipped setae is set apart from a group of more robust projections with simple and coarsely serrate morphologies (Fig. 19I–L). A third specimen (not figured) bears an array of more than 20 bulb-tipped setae of varying size.

**Remarks.** Individually, the bulb-tipped setae are broadly similar to various arthropodan cuticular projections with predominantly sensory, secretory or respiratory (rather than mechanical) roles. Modern counterparts include the aesthetascs of various crustaceans (e.g. Hallberg et al. 1992; Pasternak et al. 2005), the sensilla of the sensory pads of notostracan gnathobases (Fryer 1988, pl. 5), the bottle-shaped openings of glands in the centipede epipharynx (Koch & Edgecombe 2008, fig. 7), and the hook-tipped, sausage-shaped gill projections in certain decapods (e.g. Batang & Suzuki 2000, fig. 2). The terminal pores on the fossil bulb-tipped setae may indicate a chemosensory function, although this is not always the case in modern crustaceans (Garm & Watling 2013). In contrast, the associated knife-like and coarsely plumose setae are clearly specialized for mechanical roles, most probably cutting and screening, respectively, indicating a multifunctional role for the overall array.

**Arrays of blunt-setule setae**

**Figure 20**

**Material.** One setal array.

**Description.** One large and robust cuticle fragment bears an extensive array of more than 370 ‘blunt-setule’ setae (= E2). The specimen is partly enrolled, but appears to consist of two elongate, tapering lobes (Fig. 20A). The blunt-setule setae are c. 70–90 μm in length and exhibit a range of gradational morphologies (Fig. 20B). Most have parallel sides and a broadly rounded tip, although some taper gently to an acute tip. All have a strictly uniserial row of blunt-tipped setules stacked along their lower-middle portion. The setules resemble one another within a seta, but vary overall between forms that are long (up to 20 μm), slender and straight, to those that are strongly recurved and distally expanded, forming blunt hooks. Aside from the blunt-setule setae, a cluster of simple setae occurs on the proximal part of the specimen, and a narrow field of fine, simple setae is seen to extend distally from one of the lobes.
Remarks. In overall topology the specimen resembles the paired triangle elements (Fig. 9), which are reconstructed as a pair of elongate, tapering, setose lobes that extend apically into a narrow, fringed strip. However, the paired triangle elements have a contrasting ornamentation of fine, simple setae. The only Mount Clark setae comparable to the blunt-setule forms are the pair of E1 setae within a filter-plate association (Fig. 12G, D).

The blunt-setule setae superficially resemble the round-tipped aesthetascs of various crustaceans (Hallberg et al. 1992) and the blunt-tipped gill filaments of certain decapods (Batang & Suzuki 2000), but are distinguished by their highly unusual setulation. Setae bearing a cluster of inflated setules have been described from the maxilliped of a hirsutiid peracarid (Jaume et al. 2006, fig. 12A), and distally expanding ‘curl-tipped’ setae occur on the oostegites of some amphipods (e.g. Zimmer et al. 2009, fig. 13). However, we have not found any modern example in which such setae occur in a dense field. Overall, it is difficult to imagine a mechanical role for the blunt-setule

FIG. 18. Arrays of compound pappose setae from the Mount Clark SCF assemblage. A–D, 142815, O35-30-4; rectangles in A and B indicate areas magnified in B and C, respectively, to show details of the compound (C17) setae with successive bifurcations (arrows in C); D shows a representative distal portion of a seta. E–H, 142816, O35-30-9; rectangles in E indicate areas magnified in F–H to show dense setulation distally (F) and branching points with truncated branches (type C18 setae) (G, H). Scale bars represent: 50 μm (A, E); 10 μm (B); 5 μm (C, F); 2 μm (D, G–H).
setae, and the specimen may represent an extensive sensory array.

**Other projection morphologies**

**Figures 21, 22**

Completing the inventory of Mount Clark cuticular projections are various spines and setae with simple, pappose or serrate morphologies that tend to occur either as isolated individuals, or attached to cuticle fragments of uncertain identity (Figs 21, 22).

A few cuticle fragments bear arrays of robust, predominantly sharp-tipped simple spines (= A5; n = 3; e.g. Fig. 21A, B), dissimilar to the linear spine arrangements in the toothed blades or the predominantly rounded spine morphologies in the robustly spinose elements (cf. Figs 5, 6). Fields of thick-walled setae with blunt, angular tips (= A10; Fig. 22K) may relate to the hockey-stick armatures (cf. Fig. 16). Pappose setae with paw-like tips (= C6; Fig. 22L) have only otherwise been observed on large rectangles (cf. Fig. 8D), whereas fields of more delicate, densely set pappose setae (= C19; Fig. 22M–O) resemble the fringes of small rectangles (cf. Fig. 8M). Fields of simple setae, some with
bulbous tips (Fig. 22P), match the A12/A13 ornamentation of paired triangles (cf. Fig. 9). An enrolled cuticle fragment possibly related to paired triangles (Fig. 22Q) bears A12 and A13 setae along with variants with modified tips, both spoon-shaped (= A15; Fig. 22R) and forked (= A14; Fig. 22S).

Among the isolated spines and setae in the assemblage are broadly triangular forms with or without an apical setule (= A1; n = 5; Fig. 21H), and exceptionally large projections up to 2.9 mm long with either short (c. 10 μm) setules, or the scars of setule insertion points (= C1; n = 65; Figs 21C–E, 22A–D). A rare variant is stouter with thinner walls (= C2; Fig. 21G). Robust setae up to 540 μm long with biserial extensions at the tip (= B4) are known from a single isolated individual specimen and a small array (Fig. 22E–H). Isolated serrate spines up to 385 μm long are prominent in the assemblage (n = 164); they variably exhibit either one or two rows of acute or rounded denticles (= B1–3; Figs 21F, 22I, J); they may be derived from large robustly spinose elements.

**DISCUSSION**

The Mount Clark SCFs from Bele O-35, 1351 m, offer an unconventional and minutely detailed view of Cambrian arthropod anatomy. In terms of abundance, diversity and concentration they exceed those from other known SCF assemblages, and lie towards the exceptional end of the taphonomic spectrum: a true ‘micro-Burgess Shale’ (cf. Butterfield & Harvey 2012). The resolution of preservation reveals even the tips and setules of setae, thus providing a much expanded inventory of cuticular projections for Cambrian arthropods. Coeval macroscopic compression fossils preserve arrays of spines and setae on appendages, resolving their positions and relative sizes (e.g. Strausfeld 2016; Vannier et al. 2018) but little of their fine-scale morphologies. Simple, pappose and plumose projections can be distinguished in Orsten-type fossils, with 10 forms identified in *Rehbachiella* (Walossek 1993, fig. 35). In contrast, the 53 categories of Mount Clark projections include forms that are rare even among modern crustaceans (e.g. saw-toothed, hockey-stick and bulb-tipped setae) and some that might be novel (e.g. compound pappose setae). Compared with the plesiomorphic appearance of many lower Cambrian arthropods at the level of gross body organization, the cuticular adaptations seen here suggest essentially modern levels of functionality at the finest scale, implying equivalent levels of underlying cellular sophistication to support their sensory, secretory and mechanical roles.

The most informative body parts in the assemblage are the mandibular molar surfaces. Based on the variability in the available sample (N = 71), they have been reconstructed as belonging to a single species of arthropod, *Masticaris fimbriata* n. gen. n. sp., with evidence for ontogenetic and right–left variation in the fossil population, and a body length of up to c. 40 mm. The broader significance of the assemblage, however, depends on the extent to which the anatomical, phylogenetic and functional interpretations of the various components can be
reconciled in a reconstruction of the living animal(s). The disarticulated nature of the SCFs presents a major challenge. Arthropods naturally disarticulate taphonomically because their cuticular sclerites are more robust than the arthrodial membranes that connect them in life. In addition, laboratory processing has the potential to break up the most delicate specimens. Even so, it is clear that most of the Mount Clark SCFs reached their present levels of disarticulation prior to burial, based on the absence of observable fossils on bedding surfaces, and the identification of specimens that became enrolled or otherwise deformed prior to sedimentary compaction (e.g. Figs 1G, 8L, 20A). The identification of 71 molars from the single 150 g sample indicates that at least 35 individuals are represented in the assemblage if the molars derive from carcasses, or somewhat fewer if there was any time-averaging of moults. The prevalence of these tough body parts could suggest a high degree of pre-burial disarticulation and concentration, perhaps through winnowing of partially decayed carcasses or moults, or, conceivably, the packaging of digestion-resistant body parts into faecal pellets that subsequently dissociated on the sea floor (see Harvey et al. 2012). However, the co-occurrence of molars in the Mount Clark assemblage with very delicate setal arrays, exemplified by extensive undeformed filter plates (e.g. Fig. 11A), suggests sea-floor decay and disarticulation without extensive transport or time-averaging. Potentially analogous mass occurrences of individuals of a single non-biomineralizing taxon are known from, for example, the Chengjiang biota (Hou et al. 2017, fig. 6.4).

Phylogenetic implications

The mandibular molar surfaces are necessarily the focus for our phylogenetic analysis, being character-rich body parts that diagnose *M. fimbriata* as a new taxon. The mandible is a key feature of modern crustaceans, myriapods and hexapods, given that it arises from a pronounced modification of the perioral appendage pair for use in food processing and sometimes food acquisition. The homology of mandibles has been robustly tested and reaffirmed over many decades, on morphological, developmental and molecular criteria (reviewed in Edgecombe 2017). An important character is the division of the gnathal edge into differentiated cutting and grinding surfaces (i.e. the incisor process, or *pars incisivus*, and molar process, or *pars molaris*, respectively). The distinctive ornamentation of the Mount Clark molars, with transverse rows of minute scales confluent with the marginal fringe, matches the structure identified by Edgecombe et al. (2003) as supporting the homology of the divided mandibular gnathal edge across myriapods, hexapods and crustaceans. On this basis, *M. fimbriata* can be minimally assigned to the total group of Mandibulata.

Beyond this, a survey of molar shape and ornamentation in modern mandibulates led Harvey & Butterfield (2008, p. 869) to suggest that a ‘discrete planar, ovoid/crescentic region... bearing rows of distally divided scales that shorten unilaterally and become confluent’ unites the Mount Clark fossils with branchiopods, malacostracans and hexapods, supporting a position among crown-group pancrustaceans. Based on the more detailed
description now available, it is clear that branchiopod crustaceans, especially anostracans, offer the closest modern analogues to the Mount Clark molars. Striking similarities range from the overall outline to the fine-scale structure and arrangement of scales and scale-rows, the differentiated dorsal field, and the asymmetry with a strong ventral fringe on the right molar.

In a strictly parsimonious treatment of the data, the detailed similarities between the Mount Clark molars and those of anostracan branchiopods could be taken to

**FIG. 22.** Additional types of spines and setae from the Mount Clark SCF assemblage. A–L, disarticulated individual spines and setae, or small arrays; see text for classifications. M–O, details of setose cuticle fragments probably attributable to small rectangles. P–S, details of setose cuticle fragments probably attributable to paired triangle elements. A–B, 142825, O35-18-6; rectangle in A indicates area magnified in B. C, 142826, O35-13-4. D, 142827, O35-28-1. E–F, 142828, O35-24-4; rectangle in E indicates area magnified in F. G–H, 142829, O35-17-1; rectangle in G indicates area magnified in H. I, 142830, O35-35-13. J, 142831, O35-37-4. K, 142832, O35-15-3. L, 142833, O35-42-8. M, 142834, O35-43-8. N, 142835, O35-41-6. O, 142836, O35-42-15. P–S, 142837, O35-42-15; R and S are details from the surface. Scale bars represent: 100 μm (A, B, D); 20 μm (C, G, I, J, L); 50 μm (E, K); 5 μm (F, M, P); 2 μm (H, R, S); 10 μm (N, O, Q).
support a branchiopodan affinity for *M. fimbriata*; however, the Cambrian age of the fossils, and their disarticulated condition, mean that alternative interpretations must also be considered. First, the recent discovery of molar-like ornamentation in the Cambrian *Branchiocaris* raises the possibility that branchiopod-type features evolved convergently in quite distantly related arthropods. In particular, the perioral structures photographed in three specimens of *Branchiocaris* cf. *pretiosa* by Aria & Caron (2017, extended data fig. 8) closely resemble mandibular gnathal edges in which the incisor has been reduced and the molar elongated, a feature otherwise known only in branchiopods. The molar-like region bears transverse lineations, although any constituent scales would seem to be below the limit of resolution. Aria & Caron (2017) interpreted *Branchiocaris* as a mandibulate with well-developed mandibles bearing a molar process, prompting a new hypothesis of arthropod evolution in which a suite of bivalved arthropods, along with *Waptia* (Vannier et al. 2018) and euthycarcinoids (Aria et al. 2021), move from positions in the euarthropod stem to total-group Mandibulata. Accordingly, the perioral appendages in all of these groups have been reinterpreted as mandibles, although only these particular specimens of *Branchiocaris* hint at a mandibular structure that could be compared to the isolated SCFs. This proposed phylogenetic framework forces some difficult questions about the evolution of various mandibulate features, including the homology of the head sclerites, appendages and brain (see discussions in Edgecombe 2017, 2020; Budd 2021). If a mandibulate affinity for *Branchiocaris* were to be rejected, based for example on its deeply plesiomorphic head structure (with a prominent anterior sclerite associated in comparable taxa such as *Odaraia* and *Canadaspis* with the insertion of the eyes; see Budd 2008, 2021), it follows that the ‘mandible’ and its molar-like features are convergent. This would undermine the recognition in fossils of the canonical mandibulate synapomorphy of a mandible with differentiated gnathal edge and lined molar (*sensu* Edgecombe et al. 2003). Even if *Branchiocaris* is accepted as a mandibulate and the figured appendages as true mandibles, its branchiopod-like gnathal edge is likely to have arisen by convergence, given the deep position of *Branchiocaris* in mandibulate phylogeny (Aria & Caron 2017) versus the comparatively derived position of branchiopods among pancrustaceans (Lozano-Fernandez et al. 2019). By extension, *M. fimbriata* cannot be closely related to both *Branchiocaris* and branchiopods.

If no other comparative fossil data were available, the molar-like SCFs in the Mount Clark assemblage might reasonably be linked to *Branchiocaris*, given their broadly comparable age and probable food-handling function. However, exceptionally preserved arthropod SCFs from elsewhere in the Cambrian record offer continuity in morphology, as well as taphonomic mode, with more definitively branchiopodan fossil mandibles. SCFs from the Earlie and Deadwood formations of Saskatchewan (Cambrian Miaolingian–Furongian series), for example, include mandibles with detailed synapomorphies linking them variously to branchiopods, copepods and ostracods (Harvey et al. 2012). In particular, the branchiopod-type mandibles in the Deadwood assemblage share broad similarities with the Mount Clark examples, but with the additional preserved branchiopod synapomorphy of a posterior ‘shoulder’, and a style of ‘tooth/groove’ asymmetry shared with anostracans. In this light, a link between *M. fimbriata* and younger Cambrian SCFs is more strongly supported than a link to the appendages of uncertain homology in *Branchiocaris*. Circumstantially, but also compellingly, both the Mount Clark and Earlie–Deadwood assemblages contain essentially identical branchiopod-type filter plates (Harvey et al. 2012, figs 3 & S4).

The exact position of *M. fimbriata* in the pancrustacean tree is difficult to establish. In contrast to the branchiopod-type mandibles among the Deadwood SCFs, there are fewer candidate synapomorphies and therefore a more cautious approach is necessary. One difficulty is that in the absence of articulated material, extinct character combinations cannot logically be recognized except on a fine scale, therefore there is the risk of assigning *M. fimbriata* to an unrealistically derived phylogenetic position (a type of shoehorning error, as discussed by Harvey et al. 2012). A second difficulty relates to the local tree topology and fossil sampling density. Particular similarities have been noted with anostracan mandibles, but given that anostracans are likely to be the sister-taxon to other branchiopods (e.g. Olsen 2009; Schwentner et al. 2018), it follows that broadly anostracan-type molars could be plesiomorphic for crown-group branchiopods if they evolved at the crown node or in the stem, and were modified to varying degrees in the other branchiopod lineages. By extension, it is plausible that broadly anostracan-like molars could be plesiomorphic for a more inclusive clade of pancrustaceans, given the well-developed molars in the taxa comprising Labiocarida, the probable sister group to branchiopods (i.e. Hexapoda plus Remipedia; Schwentner et al. 2018); conceivably branchiopod-type filter plates are more deeply nested, too. Although less parsimonious by a few steps, these scenarios are difficult to reject confidently without knowledge of the respective stem groups of hexapods, remipedes, Labiocarida, or the wider clade including branchiopods (Athalassocarida *sensu* Lozano-Fernandez et al. 2019). Given that much of the deeper pancrustacean tree is essentially unsampled by fossils, we urge caution in using *M. fimbriata* to calibrate branchiopod evolution. Overall, however, a clear implication of the emerging SCF record is that a genuine radiation of comparatively derived pancrustaceans was taking place in the Cambrian, rather than multiple parallel convergences by hymenocarines on crown-pancrustacean-
type morphologies, regardless of whether the hymenocarines lie in the euarthropod or the mandibulate stem.

Reconstruction of the feeding apparatus

Any interpretation of the feeding ecology in *M. fimbriata* must focus on the molars, because they are the only body part to be formally included in the diagnosis. Importantly, however, none of the co-occurring arthropod SCFs conflicts with a reconstruction as a centimetric branchiopod-like pancrustacean, either in size or morphology, and many can be expected to occur together in functional interdependence (see below). Considering too their repetitive occurrence and restricted variability in the assemblage, we suggest that all of the major components of the Mount Clark assemblage can be plausibly assigned to *M. fimbriata*, although with varying levels of confidence. The following reconstruction should be tested through future discoveries of articulated material, or patterns of co-occurrence in other SCF assemblages.

Several components of the assemblage, including the molars, filter plates and scraping devices (saw-toothed and hockey-stick armatures), represent specialized structures adapted for the precise handling of fine food particles. In modern crustaceans the functioning of comparable components relies on coordinated interactions with adjacent body parts. The extensive, ornamented molar surfaces indicate a style of mandibular musculature and associated range of movement that would make them unsuitable for direct food acquisition, but reliant instead on food being passed forward from more posterior appendages (e.g. Snodgrass 1950). Because elongate, finely ornamented molar surfaces are associated with microphagy in extant anostracans, the food being passed to the molars is likely to have consisted predominantly of fine particles rather than bulky or unprocessed material. This would have required the co-specialization of one or more pairs of post-mandibular appendages for the handling of fine particulate food. Similarly, the Mount Clark filter plates and scraping devices can only have been functional in conjunction with antagonistic armatures able to gather the collected particles and pass them towards the mouth: in modern crustaceans, particle-handling relies on mechanical manipulation rather than movement by water currents (Fryer 1983, p. 300; Schabes & Hamner 1992). Rare articulated specimens from the Earlie–Deadwood assemblage confirm that Mount Clark-type filter plates and saw-tooth setae do indeed occur together on branchiopod-type lobate appendages (Harvey *et al*. 2012, figs 3 & S4). We suggest that in the Mount Clark assemblage, at least, they come from *M. fimbriata*. The alternative is that there is more than one taxon in the Mount Clark assemblage with an intricate, branchiopod-type feeding apparatus. This is possible, but would raise further questions: what taphonomic mechanism would bring together the mandibles of one taxon with the legs but not the mandibles of another?

For the more robust armatures and articles in the assemblage, there are fewer constraints on function or body position, therefore their relation to *M. fimbriata* is more speculative. As discussed above, however, there are similarities between branchiopodan thoracic endites and/or endopods and the Mount Clark hockey-stick armatures, toothed blades, and many of the robustly spinose elements. Furthermore, the paired triangles compare well to the anterior sternal regions of branchiopods. Insofar as these comparisons have been made independently of any interpretive model arising from the molars, the consistency of the interpretation is notable.

Considered as a whole, the Mount Clark arthropodan SCFs are most parsimoniously reassembled as a single functioning feeding apparatus. The mandibular molar surfaces would have processed the food immediately prior to ingestion, with the anterior tuft of setae positioned to push food into the oesophagus, accompanied by sucking movements from the mouth. The paired triangles, reconstructed as the sternal region, would have aided in directing the food forwards, along with the labrum (which has not been clearly identified in the assemblage). The various more delicate armatures, including the filter plates and the finer pappose setae, would have been suitable for preparing the particles, via size sorting and screening, for trituration on the molar surface. The filter plates could also have gathered suspended particles directly from the water column. More robust armatures suitable for a role in scraping or pounding a substrate include the robustly spinose elements, hockey-stick armatures, and the toothed blades. Following a branchiopodan model, these elements could have been borne as endites and/or endopods on thoracic appendages, perhaps distally on the same appendages as the filter plates (cf. Hegna & Lazo-Wasem 2010). Rhythmic movement of these limbs would have acted to generate and capture particles while simultaneously cleaning one another (perhaps involving the saw-toothed armatures) and manoeuvring the food mechanically forwards along a food groove floored by sternites (the small fringed rectangles).

Implications for diet and ecology

The function of any particular arthropodan armature or body part depends to a large extent on its positional and behavioural context, making the functional interpretation of disarticulated feeding apparatus particularly challenging. Even so, the detailed preservation of the Mount
Clark fossils allows a number of substantial inferences to be drawn. On their own, the molar surfaces indicate that *M. fimbriata* had a predominantly microphagous habit, with the various associated elements not only corroborating this view but pointing to considerable versatility in feeding behaviour and diet: for example, substrate-scraping armatures for generating food particles, coupled with intricate filtering devices capable of efficient suspension-feeding. The diversity of cuticular projections in the assemblage, comprising at least 53 categories (Fig. 4, Table 1), far exceeds previous inventories for Cambrian arthropods, individually or collectively. If most (or even many) of these originated from *M. fimbriata*, it implies an exceptionally high level of trophic versatibility. Even within individual armatures there can be an impressive variety of projections: the filter plates alone contain 11 different types, including both robust and delicate morphologies. In modern crustaceans, for example, suspension- and deposit-feeders are expected to have a higher setal diversity than predominantly carnivorous or scavenging crustaceans (Watling 2013). Moreover, a study of living thalassinid shrimps found that a high setal diversity, especially of robust and serrate forms, corresponds to a variance in diet and processing ability that is more typical of generalists or deposit-feeders than of dedicated suspension-feeders (Coelho & Rodrigues 2001). By extension, a wholly planktic, suspension-feeding ecology for *M. fimbriata* appears less likely than a mixed, nektobenthic lifestyle. Comparable ecologies are typical of living large branchiopods with diverse thoracic armatures (e.g. Mura 1995).

**Comparisons to feeding in other Cambrian arthropods**

The feeding structures of *M. fimbriata* are strikingly intricate: they provide direct evidence for armature differentiation within appendages, and strongly imply differentiation between adjacent appendages, most obviously between the mandible and its neighbouring limbs. By contrast, many Cambrian arthropods have low levels of differentiation both within and between appendages, implying comparatively simple and imprecise feeding styles. Raptorial feeding using a frontal grasping appendage has been reconstructed for many lobopods, radiodonts and great appendage arthropods, whereas gnathobasic feeding typifies almost everything else, indicated by an essentially homonomous series of post-antennular appendages with spiny leg bases (Bouzfield 1995; Budd 2001). Neither style requires diverse projection morphologies, integrated setal armatures, or prominent appendage tagmosis (Budd 2001), although certain Cambrian stem-euarthropods and even lobopodians show interesting departures from a homonomous appendage series (e.g. Zhai et al. 2019b; Yang et al. 2015), and Cambrian gnathobases were impressively diverse in shape, ornamentation and function (e.g. Bicknell et al. 2018, 2021). Even so, the most intricate and sophisticated appendages among Cambrian arthropods belonged to mandibulates.

Among the Cambrian arthropods known from whole-body fossils, the highest degrees of appendage tagmosis occur in the candidate mandibulate hymenocarines (sensu Izquierdo-López & Caron 2021, fig. 8). Generally, the mouthparts are not resolvable to a level that permits comparison with *M. fimbriata*, either because they are obscured by other head structures or because they are simply not well enough preserved. In many taxa, however, it is evident that the trunk limbs are essentially homonomous and constructed from repetitive units, implying low levels of armature differentiation. One notable exception is *Waptia*, which has appendages interpreted as antennules, mandibles and maxillules, a series of cephalothoracic appendages and a contrasting series of lamellate appendages, plus a limbless abdomen and a tail fan (Vannier et al. 2018). This strikingly crustacean-like tagmosis suggests a high degree of sophistication in feeding and other functions. Among the mouthparts are appendage lobes with specialized armatures, frequently with variation along the limbs as well as between them. As noted above, some of the armatures, such as those on the distal mandibulate palp (Vannier et al. 2018, fig. 8c,d), resemble the more robustly spinose Mount Clark fossils, although nothing appears to be an exact match. Importantly, the superficially filter-like posterior appendages are actually composed of imbricating, round-tipped lamellae rather than a meshwork of plumose setae (Vannier et al. 2018, fig. 16); they are unlikely to have been involved in feeding. Therefore, there is nothing to suggest that *Waptia* is closely related to *M. fimbriata*, although both demonstrate a level of anatomical sophistication that is far beyond that of most Cambrian arthropods.

Of particular interest are the filter plates (coplanar plumose armatures) in the Mount Clark assemblage, and the question of whether anything comparable occurs in Cambrian macrofossils. Many hymenocarines have long series of closely spaced thoracic appendages that are reminiscent of branchiopod-type filtering limbs. On closer inspection, however, they lack evidence for appropriate armatures along the midline, which in branchiopods is where the food-handling takes place. This discrepancy has long been recognized as evidence against a close phylogenetic link to branchiopods, and a challenge for reconstructing the true feeding mechanism (including in Branchiocardia; see Briggs 1976). Nevertheless, suspension feeding is often assumed for taxa with long series of thoracic appendages (reviewed in Legg et al. 2012; see also Izquierdo-López & Caron 2020, 2021), although without specialized endites this...
must have been very inefficient (as noted by Legg et al. 2012; see also Budd 2001). More broadly, the challenge with invoking suspension feeding in Cambrian panarthropods is not only explaining how food particles were captured, but how they were then transferred to the mouth and ingested. For example, it has been suggested that Isoxys used orally directed water currents (Vannier & Chen 2000, p. 304), and that Marrella used the tips of inner trunk-appendage rami to pick up particles trapped on the setose outer rami (García-Bellido & Collins 2006); both mechanisms lack modern analogues. The way in which particles might have been transferred to the mouth in purported suspension-feeding lobopodians (e.g. Yang et al. 2015; Caron & Aria 2017) and radiodonts (e.g. Vinther et al. 2014) is even more mysterious, but presumably required direct interaction of the appendages with the mouth. Unless this transfer was reasonably efficient, the functional mesh size of any proposed filter seems of secondary importance. In contrast, the Mount Clark filters, scrapers and fringed molars show that some Cambrian arthropods were operating at essentially modern levels of sophistication.

Elsewhere in the Cambrian fossil record, Orsten-type assemblages offer a detailed window onto very small-bodied Cambrian arthropods, preserving three-dimensional feeding apparatuses of individuals measuring up to 2 mm in length. Most Cambrian arthropods of this size were presumably restricted to feeding on very small particles (except for non-feeding larvae, fluid-feeding pycnogonids, and the possibly parasitic, pentastomid-like fossils: see Walossek et al. 1993; Waloszek & Dunlop 2002; Waloszek et al. 2006). Agnostids and Oelandicaris may have gathered suspended detrital material with their antennules (Müller & Walossek 1987; Stein et al. 2005, 2008). Most other crustacean-like Orsten taxa are likely to have simply swept particles towards the mouth using only the pre- and peri-oral appendages (e.g. Martinsonia and Bredilocaris; Müller & Walossek 1986, 1988).

More complex post-oral ‘filter-feeding’ mechanisms have been proposed for the Orsten arthropods Skara and Rehbachiella (Müller & Walossek 1985; Walossek 1993). In Skara the feeding apparatus consists of a cage-like arrangement of the four poorly differentiated, posterior appendage pairs (Müller & Walossek 1985, fig. 16). Although the medial endites are well-adorned with orally directed setae that would undoubtedly have helped in retaining particles and transmitting them to the mouth, there are no filter plates as strictly defined, and the setal diversity is low. By contrast, Rehbachiella had a substantially differentiated particle-feeding apparatus, and provides the closest Orsten comparison to the Mount Clark fossils. Along with a prominent mandible that is divided into molar and incisor processes, Rehbachiella exhibits a modest setal diversity, and a set of particle-handling adaptations that support a phylogenetic relationship to branchiopod crustaceans (Walossek 1993; Olesen 2009). The feeding mechanism features a deep food groove associated with a long series of thoracic appendages that bear many prominent, densely setose and posteriorly orientated endites along their medial surfaces (Walossek 1993, p. 105). However, in contrast to the strictly defined, coplanar filter plates seen in the Mount Clark assemblage, the enditic armatures of Rehbachiella consist of subparallel arcs of setae with only moderately fine intersetule distances of 2 µm in the biserially serratate and plumose forms (Walossek 1993, p. 57). This arrangement is consistent with particles being transported anteriorly via the mutual lifting and catching actions of adjacent appendages during metachronal motion, a feature common to the thoracic filtering devices of extant branchiopods and leptostracans. However, there are also similarities to extant cephalocarids (Walossek 1993, p. 103), which can be considered ‘particle-shufflers’ but not filter-feeders (Sanders 1963). Indeed, Rehbachiella resolves as a stem-cephalocarid rather than a branchiopod in one detailed cladistic analysis (Wolfe & Hegna 2014). Whatever its phylogenetic affinity, it is notable that the enditic armatures both within and between the thoracic appendages in Rehbachiella vary along gradients of size and number rather than among regions of differentiated morphology, and that the setal diversity (Walossek 1993, fig. 35) is substantially lower than in the Mount Clark filter plates.

More generally, it is probable that body size explains much of the complexity difference between the Mount Clark individuals, which attained centimetric dimensions, and the millimetric Orsten specimens (Harvey & Butterfield 2008; Harvey et al. 2012). It is widely observed that setal diversity tends to increase through ontogeny (e.g. Lavalli & Factor 1992; Cox & Johnson 2003). Millimetre-sized crustaceans live in environments where Reynolds numbers (Re) can be extremely low, meaning that small, slow-moving structures such as appendage lobes and food particles are associated with relatively thick boundary layers of viscous water, with the implication that minute variations in setal morphology cannot always be expected to be functional (Koehl 1996). Microcinematography and fluid-mechanic modelling of extant planktic copepods, for example, shows that individual particles (such as unicellular algae) are typically grasped along with the parcel of water in which they are effectively contained using fans of setae (not strict filter plates) on the maxillae (e.g. Koehl & Strickler 1981; Koehl 1995; reviewed in Watling 2013). Below a certain Re threshold, these appendages behave as solid paddles rather than leaky sieves or filters, and a selective diet is achieved simply by pushing away particles judged to be unsuitable on chemosensory criteria. By contrast, larger crustaceans do not have the option of handling minute particles individually, and therefore require more complex machinery if they are to harvest, sort and ingest particulate food. At the same time, subtle variations in the faster-moving setae will become functional.
and can be selected for. At several centimetres long, *M. fimbriata* had vastly different physical requirements from the arthropods preserved in Orsten-type assemblages, therefore it is not surprising that it possessed fundamentally more intricate cuticular adaptations.

Given the influence of body size on functional morphology, and because the smallest mandibles known from *M. fimbriata* are larger than any described for *Rehbachiella*, which is the only current candidate for a whole-body Cambrian branchiopod, it has to be asked whether the two forms might represent different ontogenetic views of a single taxon. It is unlikely: there is no evidence of Mount Clark-type molar surfaces, coplanar filter plates, scraping devices, or a comparable diversity of cuticular projections in *Rehbachiella*, and its anagenetic mode of development (Walossek 1993) gives no reason to suspect a radical ontogenetic transformation.

Overall, it is difficult to identify anatomical links between Cambrian mandibulates preserved as Burgess Shale-type macrofossils, Orsten-type microfossils, and SCFs. In part, this is likely to reflect the different levels of resolvable detail preserved in each assemblage, combined with anatomical changes occurring through ontogeny, linked to functional constraints. To an important degree, however, it seems that the three taphonomic modes are sampling different facets of Cambrian arthropod diversity.

The evolution of crustacean feeding ecologies

For all their morphological specialization, the Mount Clark feeding structures appear to have belonged to a dietary generalist. This seemingly incongruous relationship between form and function has also been noted in modern crustacean ecology. In general, crustacean feeding is often difficult to classify, whether by diet (carnivory, herbivory etc.), food size (microphagy vs macrophagy), or feeding mode (predation, scavenging etc.) (Dauby *et al.* 2001, p. 71; Grahame 1983; Watling 2013). Although Marshall & Orr (1960) distinguish classes of filter feeders (suspension and detritus feeders), scavengers, predators and parasites, they note (p. 228) that these ‘have no rigid limits; one grades into another, and one animal may belong to more than one group’, and conclude (p. 253) that ‘few Crustacea are specialized feeders; most will take anything edible that comes their way, and a number have more than one kind of feeding mechanism’. Cisne (1974, p. 341) discussed possible reasons why ‘crustaceans from cephalocarids to crabs very often feed none too selectively on what appears to be the same detritus, as if their widely differing degrees of limb tagmosis made no difference whatever in feeding specialization’. The nature of crustacean feeding systems often means that the ecological interpretations of fossil taxa seem rather vague. Unfortunately this tends to obscure the fundamental differences between crustaceans and the genuinely unspecialized generalists that dominate Cambrian arthropod assemblages (see also Budd 2001, p. 408).

Importantly, the distinction of crustacean feeding systems lies in their versatility, not only across the group as a whole, but within individuals. High degrees of plasticity in individual feeding reflect an ability to deal efficiently (not just adequately) with many different sources of food; see for example Hunt *et al.* (1992) on penaeid prawns with a preference for macrophagous feeding but the ability to feed on much smaller particles if necessary. The apparent correlation in many crustaceans between morphological specialization and dietary generalism, which seems to contradict predictions of niche partitioning, arguably has parallels in Liem’s paradox, which expresses the same concept applied, originally, to cichlid fish (Liem 1980; see also Robinson & Wilson 1998). Part of the solution in crustaceans is that, as Cisne (1974) emphasized, dietary differentiation among similar species can be subtle and difficult to observe, reflecting fine-scale food-sorting by mouthparts, differences in feeding behaviour or dietary preference, and differences in digestion and nutrient utilization. Indeed, studies of niche partitioning in extant crustaceans often have to draw on multiple lines of evidence to resolve particular feeding habits, with morphological observations supplemented by, for example, analyses of gut contents, digestive enzymes, and stable isotope composition (e.g. Dauby *et al.* 2001; Guisande *et al.* 2002; Johnston & Freeman 2005; Winkler *et al.* 2007).

The Mount Clark feeding structures can be reconstructed as coming from a centimetric ‘specialized generalist’ that possessed the necessary complexity to process a variety of food sources, selectively if required, with a degree of efficiency not available to other Cambrian arthropods of comparable size. The many intricate cuticular specializations in the assemblage prefigure the long-term trend in crustaceans for morphological differentiation within and between appendages and body regions (tagmosis): modern crustaceans tend to have high degrees of appendage specialization and corresponding trophic diversity (e.g. Cisne 1974; Budd 2001; Adamowicz *et al.* 2008), whereas the few remaining aquatic eucarid crustaceans (i.e. xiphosuran horseshoe crabs) retain a gnathobasic feeding style and have predatory or poorly selective detrivorous ecologies (e.g. Manton 1964).

CONCLUSION

Exceptionally preserved SCFs from the Mount Clark Formation include a rich array of disarticulated body parts that offer an unrivalled view of microscopic anatomical innovations among early Cambrian arthropods,
complementing Burgess Shale-type macrofossils and Orsten-type microfossils. Distinctively elongate and fringed mandibular molar surfaces define a new taxon, Masticarid fimbriata. The molars show intricate similarities to those of branchiopod crustaceans, and a resemblance to structures on the perioral mouthparts of Branchiocaris. Anatomical links to younger Cambrian SCFs, which show additional branchiopodan characters, and co-occurrence with other body parts not seen in Branchiocaris or other Cambrian fossils, suggest that M. fimbriata represents an early pancrustacean, and possibly a total-group branchiopod, rather than a hymenocarid. The Mount Clark molars indicate a centimetric adult body size for M. fimbriata, and a dietary ecology involving the precise handling of fine food particles. An analysis of functional morphology supports a common provenance for many of the associated SCFs, but with differing degrees of confidence. Co-occurring filter plates and fine scraping armatures almost certainly belong to M. fimbriata, with their probable functional interdependence suggesting advanced suspension-feeding capabilities. Beyond this, co-occurring body parts with robustly spinose armatures, connecting in turn to hockey-stick armatures, probably belong to M. fimbriata, in which case its ecology is likely to have included nektobenthic particle generation rather than solely planktic particle collection. Whatever M. fimbriata was choosing to eat at any particular moment, it would have done so in a precise and controlled manner: a prevailing ecological strategy among crustaceans.

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SUPPORTING INFORMATION

Additional supporting information can be found in the online version of this article (https://doi.org/10.1002/spp2.1458):

Table S1. Specimen numbers for figured specimens and slide locations for mandibles.

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