Gill grooming in middle Cambrian and Late Ordovician trilobites

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Abstract

Efficient extraction of oxygen from ambient waters played a critical role in the development of early arthropods. Maximizing gill surface area enhanced oxygen uptake ability but, with gills necessarily exposed to the external environment, also presented the issue of gill contamination. Here we document setae inserted on the dorsal surface of walking legs of the benthic-dwelling middle Cambrian *Olenoides serratus* and on the gill shaft of the Late Ordovician *Triarthrus eatoni*. Based on their physical positions relative to gill filaments, we interpret these setae to have been used to groom the gills, removing particles trapped among the filaments. The coordination between setae and gill filaments is comparable to that seen among modern crustaceans, which use a diverse set of setae-bearing appendages to penetrate between gill filaments when grooming. Grooming is known relatively early in trilobite evolutionary history and would have enhanced gill efficiency by maximizing the surface area for oxygen uptake.

1. Introduction

Early metazoans required sufficient oxygen to enable their complex morphologies and lifestyles, and their appearance in the fossil record coincides with rising but fluctuating oxidation conditions of the early Palaeozoic oceans (Wood & Erwin, 2018). Gills – organs specialized in transferring oxygen from the external medium to the interiors of animals – appeared by the early Cambrian and played an important role in the biodiversification of early metazoans (Raff & Raff, 1970). Structures exposed to the external environment are liable to pollution and damage, and actions that maintain their efficient functioning likely offered advantage. Among living aquatic animals grooming is considered to be a 'secondary behaviour' undertaken when 'primary behaviours', such as feeding, mating and fighting, are not being conducted (Vanmaurik & Wortham, 2014). One of the principal functions of grooming in arthropods is to clear the gills so as to maximize the surface area available for oxygen uptake (Wortham & Pascual, 2017), and it is regarded as a task essential for survival (Pohle, 1989). However, grooming has rarely been discussed with respect to the early arthropod fossil record (Fortey & Owens, 1999; Waloszek, 2003; Stein *et al.* 2005), and gill grooming has only been proposed in a single Silurian ostracod, *Spiricopia aurita* (Siveter *et al.* 2018). Here we investigate the appendicular details of two trilobites, the middle Cambrian *Olenoides serratus* and the Late Ordovician *Triarthrus eatoni*, and suggest how their gills were cleaned.

2. Materials and methods

Materials described in this paper are housed in the Geological Survey of Canada (GSC), Ontario, Canada; The Hunterian Museum, University of Glasgow (GLAHM), UK; the National Museum of Natural History (NMNH) of the Smithsonian Institution, Washington, DC, USA; and the Yale Peabody Museum of Natural History (YPM), Yale University, USA.

The pyritized specimens of *Triarthrus eatoni* are from the Beecher's Trilobite Beds of the Katian (Late Ordovician) Frankfort Shale of upper New York State, USA, and the Katian Whetstone Gulf Formation ('Martin Quarry') (Briggs *et al.* 1991; Farrell *et al.* 2009). Specimens of *Olenoides serratus* are from the Burgess Shale Biota of the middle Cambrian (Wuliuan Stage) Burgess Shale Formation (previously known as the Stephen Formation) of British Columbia, Canada (Briggs *et al.* 1994). The limbs of both these trilobite species show a consistent morphology along the anterior–posterior body axis, except for specialized limbs recently interpreted to represent sexual dimorphic features (Losso & Ortega-Hernández, 2022), and differ slightly in size (Whittington, 1975; Whittington & Almond, 1987). Of *c.* 250 specimens examined by us either directly or as images, few show the necessary combination of well-exposed setae on both walking legs or gill shafts, and gill filaments, which are necessary for assessing the relationship between setae and their associated gill branch and for providing

Fig. 1. Illustration of the measurement terms used in this paper: (a) reconstruction of the partial gill branch of *Triarthrus eatoni* showing the filament length and filament gap; (b) reconstruction of the partial walking leg of *Olenoides serratus* showing the setal diameter, setal gap and setal length. Abbreviations: fg, filamental gap; fh, filament height; fl, filament; fll, filament length; fw, filament width; sd, setal diameter; sg, setal gap; sh, gill shaft; sl, setal length.
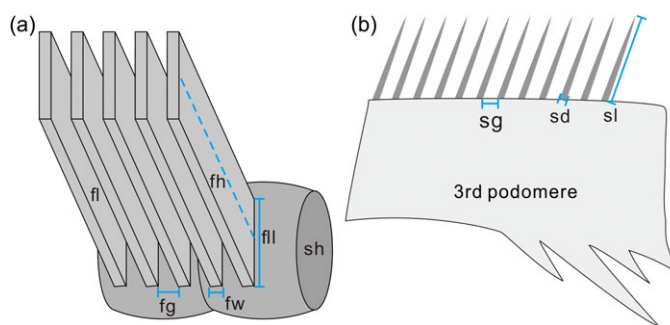
relative size data. The clearest insights come from limbs preserved in incomplete specimens (GSC 34692, 34695, 34697; USNM 65514). For this reason, we cannot identify the particular trunk segment to which the limbs described belong, except in USNM 65513 (and its counterpart USNM 58590) in which the limb is the third cephalic biramous appendage (Whittington, 1975). The terms walking leg and gill branch used in this paper follow Whittington (1975) and we use them because they simplify our discussion of functionality.

Here, filament length (fll; Fig. 1a) is measured along the dorso-ventral axis where the filament contacts the gill shaft or lobe, as this direction closely mirrors the long axis of the dorsoventrally pointed setae of the walking legs. The long axis of the filament we refer to as filament height (fh; Fig. 1a). Filamental gap (fg; Fig. 1a) is measured along the proximal end of the filaments, which is near the shaft or lobe of the gill branch. The extent of the filamental gap is measured between the margins of adjacent filaments (Fig. 1a), where its length is least affected by taphonomic compression. The interfilament interval is the combination of the thickness of one filament measured across the inflated, dumbbell-shaped end (corresponding to the end of the inflated marginal bulb of the filament, as described in Hou *et al.* (2021)) and one filamental gap. Setal gap (sg; Fig. 1b) is measured along the podomere of the walking leg. Setal diameter (sd; Fig. 1b) is measured along a line that is perpendicular to the seta itself or to setal length (sl; Fig. 1b). Setae have clearly exposed boundaries (light-coloured matrix in figures) that are parallel to each other and thus serve well for measurement of setal diameter.

The specimens were photographed using a Canon EOS 50D with Canon EF-S60 mm lens, Leica MZ16 with DFC420 lens, Leica M205C with DFC 700T lens, Opto-Digital Microscopy and PHILIPS XL-30 Environmental Scanning Electron Microscope (ESEM). The Opto-Digital Microscopy and Leica M205C is installed with a stack or non-stack function. The ESEM was used with both backscattered-electron (BSE) and gaseous secondary electron (GSE) techniques, which are described in the figures. Figures were prepared using CorelDRAW 2018. For more information see Hou *et al.* (2021).

3. Results

3.a. Olenoides serratus

The endopod (walking leg) bears setae on the dorsal surface of its third to fifth podomeres (Whittington, 1975). Podomeres 3 and 4 are preserved close to the distal margin of the gill branch. Podomeres 3, 4 and 5 bear as many as 14 (calculated based on the number of visible setae and the length of podomere 3 in Fig. 2d), 15 (Fig. 2b, d) and 3 (Fig. 2c, d) setae, respectively, inserted

on their dorsal surfaces. Podomere 2 may also have borne dorsal setae, as one possible example is recognized (Fig. 2d) although confirmation of this is difficult in these two-dimensionally preserved specimens. The length of the setae is *c.* 2.5 times (observed in five specimens) the length of the opposed filaments on the other branch of the same biramous limb. Measuring the well-preserved appendages (Fig. 2a) shows that the filaments are arranged *c.* 0.28 mm apart, and the dorsal setae on the walking leg are arranged *c.* 0.25 mm apart and are each *c.* 0.15 mm in diameter. Each gill filament also bears a group of setae distally, about five in total, which are slightly shorter than the filament length (Fig. 2j–l). The distal lobe of the gill branch bears setae that are approximately four times longer than the filament setae (Fig. 2j).

3.b. Triarthrus eatoni

In contrast to the walking leg setae of *O. serratus*, *T. eatoni* had setae on the shaft of its gill branches (Fig. 3a–h). Most proximal shaft articles apparently bore one seta (Fig. 3a–e), but there were possibly two or more in each article on the distal shaft articles (Fig. 3f–h). The terminal spoon-shaped article of the shaft, actually consisting of many separate narrow articles (Fig. 3d–f), bore many spines surrounding its margin (anterior, distal and posterior), forming a terminal brush-like structure (Fig. 3f–h). The length of setae on the gill shaft is about four times the length of associated filaments. The diameter of the setae is about half of the interfilament interval.

4. Discussion

4.a. Grooming gill filaments

In *Olenoides serratus*, the distal lobe of the gill branch partly overlapped the third podomere of the walking leg (Fig. 2a), thus the majority of the gill branch was not located directly above the dorsal setae, which are on podomeres 3 to 5. The mismatch between gill filaments and dorsal setae means that these two structures were not in direct contact when the appendages were prone. However, with rotation of walking legs during the walking motion, these dorsal setae moved in relative position. Anterior or posterior rotation of the walking leg positioned both podomeres 3 and 4 beneath the gill filaments, and thus the dorsal setae could penetrate between the gill filaments (Fig. 4a). This interaction between the dorsal setae and the gill filaments achieved the grooming function. This is consistent with evidence that a slightly narrower interval between dorsal setae than between gill filaments allowed each slim seta to penetrate into the gaps between filaments, which had a relatively wide interval, possibly permitting every interfilament channel to be cleaned. The distal setae of the filaments themselves (Fig. 2j–l) may have provided additional aid in grooming the gill filaments of the
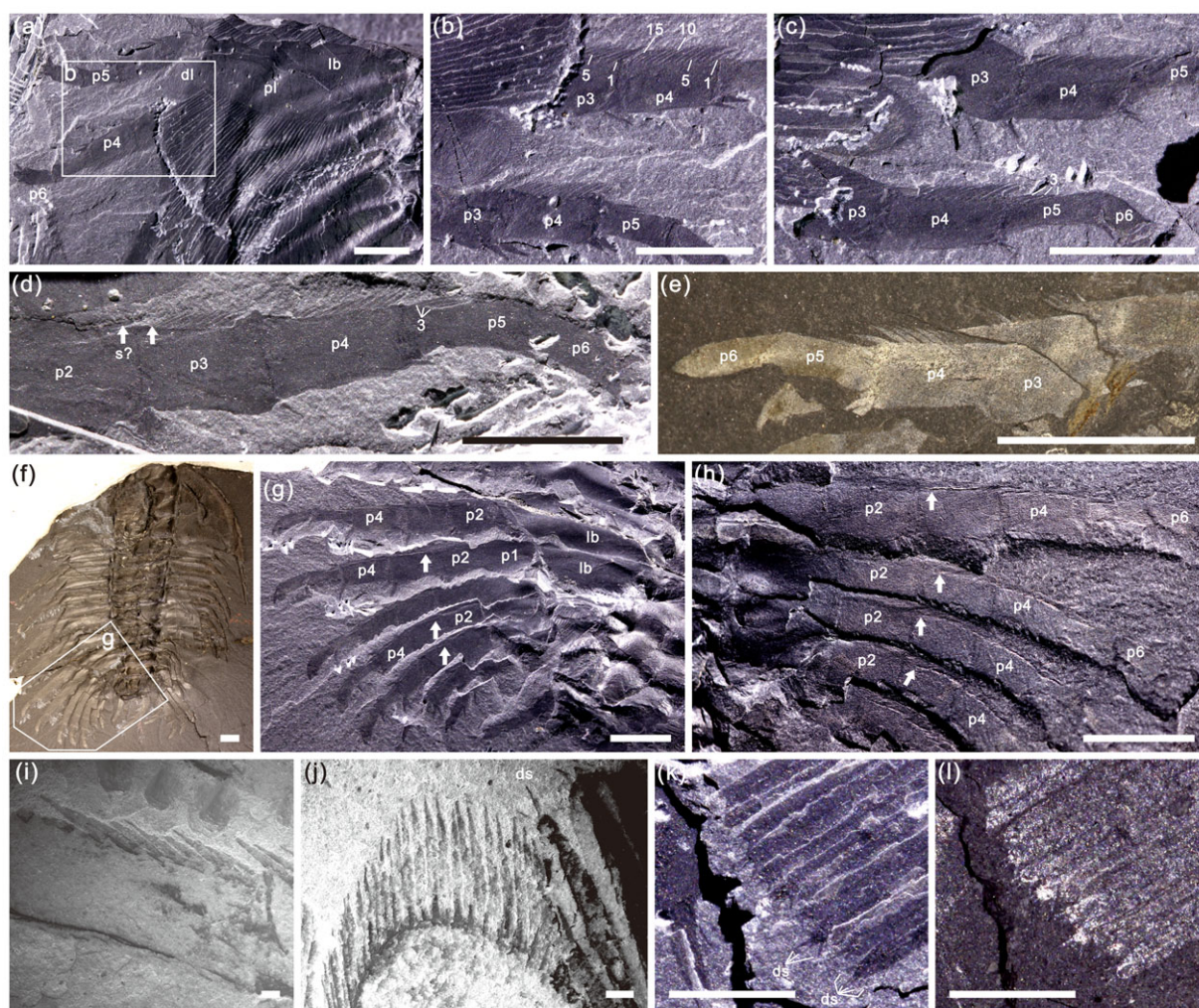
Fig. 2. Setae on appendages of *Olenoides serratus*: (a–c) dorsal setae of walking legs, GSC 34695a – (b) has been rotated 180° with respect to (a); (d) dorsal setae of walking legs, GSC 34697; (e) dorsal setae of walking legs, GSC 34694; (f–h) dorsal setae of walking legs, USNM 58589; (i–j) setae on both walking leg and gill branch, USNM 65514; (k–l) distal setae of gill filaments, GSC 34697. Arabic numbers mark the number of setae. White arrows point to dorsal setae. Abbreviations: dl, distal lobe of the gill branch; ds, distal seta of the gill filament; lb, limb base of the walking leg; pl, proximal lobe of the gill branch; p1–6, podomeres 1 to 6, respectively. Scale bars: 0.2 mm (i, j); 2mm (k, l); 5 mm (a–h).

adjacent appendage by working together with the dorsal setae of the walking legs.

The possible seta (Fig. 2d) and linear impressions (Fig. 2g–h) on podomere 2 hint that there may have been additional setae on the dorsal surface of that podomere and possibly also on podomere 1. As the appendages decrease in size posteriorly along the trunk (Whittington, 1975; Whittington & Almond, 1987), it is possible that the number of dorsal setae varied among walking legs, but during rotation all dorsal setae of the walking legs were located closely beneath the gill filaments in the necessary posture for grooming. In contrast, the ventrally located endite spines of the walking legs are considered to have been used for processing food and their location prevents them having been used in grooming the gill filaments.

In *Triarthrus eatoni*, setae are developed not on the walking leg, but along the gill shaft itself, where a single seta is located near the distal end of each article. We envisage a situation in which these setae groomed the gill filaments of the appendage preceding them (Fig. 4b). The diameter of the grooming setae is about half of the interfilament interval, meaning that the seta is wider than the gap near the inflated dumbbell-shaped ends, with the thickness of these

ends about twice the filament gap (Hou *et al.* 2021). However, the ratio of the setae to filaments is about 1:3. A small number of setae compared to filaments would allow setae to easily penetrate into the filament gaps, and we envisage some flexibility amongst filaments, that may have temporally compressed together during grooming. Thus, each seta may have serviced several adjacent filaments via a series of grooming sweeps. This grooming form and function is clearly distinguished from that of *O. serratus*.

In both species, the grooming setae, being distinctly longer than the length (dorsal–ventral direction) of the filaments, allowed them to pass between and extend beyond the filaments, effectively extruding particles trapped between adjacent filaments (Fig. 2a–l, 3a–h, 4a–b). Coordination between the grooming setae and the gill filaments apparently worked to remove fouling material from the surface of the gill filaments (Fig. 4a–b). The two different positions of setae studied herein may suggest that multiple solutions to gill fouling evolved among trilobites. Among modern arthropods, particularly crustaceans, grooming is an activity pursued on a necessarily daily basis. Crustacean gill filaments are relatively fragile and are located in concealed positions, and these
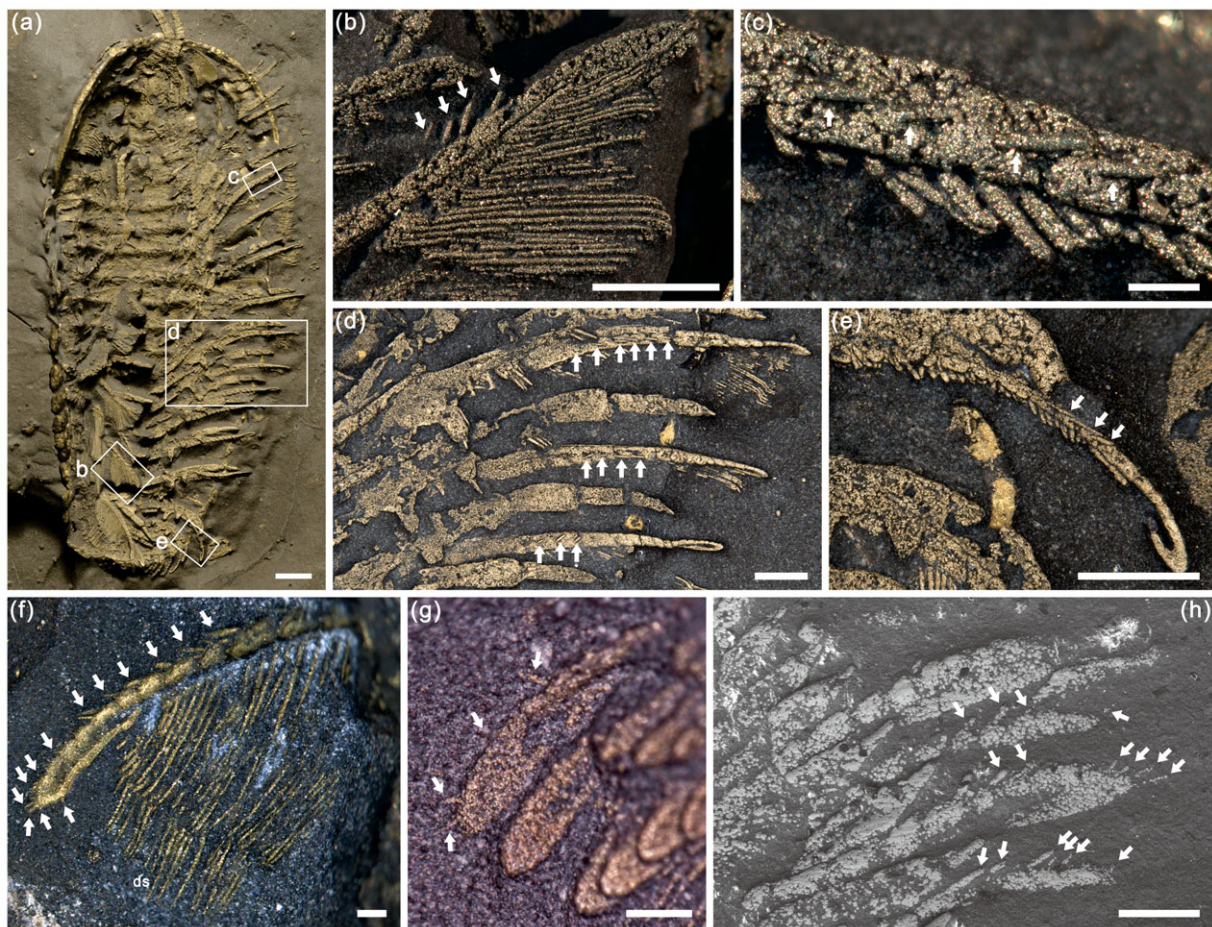
Fig. 3. Grooming setae of *Triarthrus eatoni* and reconstructions of grooming behaviour: (a–e) *T. eatoni*, GLAHM 163103, close-up of shaft setae in (b–e) being marked in (a); (f) *T. eatoni*, setae on the margin of gill shaft and the distal portion of the gill filaments, YPM 220; (g) setae on the gill shaft of *T. eatoni*, USNM 65527; (h) setae on the gill shaft of *T. eatoni*, USNM 400932. White arrows point to shaft setae. ds, distal seta of the gill filament. Scale bars: 0.2 mm (c, f–h); 1 mm (b, d, e); 5 mm (a).

animals use a diversity of structures to perform grooming, e.g. the epipod (Bauer, 1981), pereiopod (Batang & Suzuki, 2003) or chela (Bauer, 1979) for gill grooming (Bauer, 2013). Coordination between the appendages and gills in modern crustaceans (Bauer, 2013) is comparable to that described above for the two trilobite species. In modern examples the grooming setae display a high diversity of morphologies (Bauer, 2013; Wortham & Pascual, 2019), suggesting varied ways of dealing with gill fouling. Perhaps likewise, here we suggest two different modes of gill cleaning among some of the only trilobite species sufficiently well preserved to permit its evaluation. Modern crustaceans can also use appendages on the right side of the body to clean gills on the left side of their bodies (Batang & Suzuki, 2003). This appears not to have been possible in these trilobites because the ventrally projected endite spines of the walking legs would have obstructed such movement. Considering that the morphology of grooming structures has played an important role in the classification of arthropods (Spruijt *et al.* 1992), further analysis of setal morphology and possible grooming behaviour among trilobites may prove to be phylogenetically informative.

4.b. Contamination source

Palaeozoic *Cruziana* or *Rusophycus* trace fossils are known to have been produced by trilobites or trilobite-like arthropods (Alpert, 1976; Seilacher, 1985; Crimes & Droser, 1992; Seilacher, 2007). Their construction via walking leg digging involved disturbing seafloor sediment, and resuspending it. Unlike decapod crustaceans that have the branchiostegite (gill chamber) to protect from gill fouling (Bauer, 1989), the openly exposed gill filaments of trilobites would bring them into direct contact with suspended sediments or particles. Thus the water flowing through gill filaments would have been rich in suspended particles that could have become trapped between gill filaments. While digging and associated food collection may have been a primary cause for gill fouling, periodic storms in the shelf settings where these trilobites lived were likely another. Biological contamination was likely another important source. There are already several cases of epibiont or symbiosis recorded in diverse Cambrian animals (Zhang *et al.* 2010; Cong *et al.* 2017; Li *et al.* 2020; Nanglu & Caron, 2021; Yang *et al.* 2021), and trilobite exoskeletons were targets for biological attachment (Brandt, 1996; Hughes, 2001; Key *et al.* 2010; Baets *et al.* 2021). In modern crustaceans, tightly arranged filaments provide other organisms the opportunity to trap particles from the respiratory stream, favouring the growth of microbial organisms and epizoites on the gill surfaces (Bauer, 1989). Without grooming, such fouling can be severely deleterious (Bauer, 2013). Given structural similarities, such conditions can both be expected to have also occurred in trilobite gill filaments.
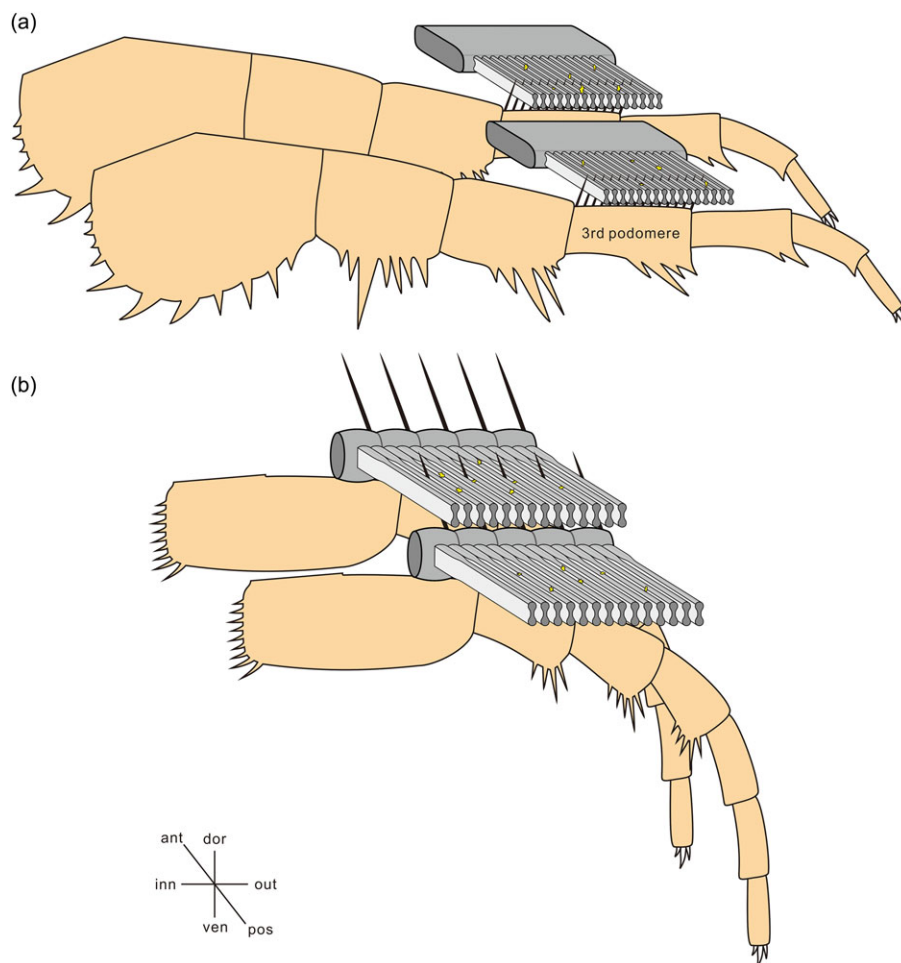
Fig. 4. Reconstructions of trilobite grooming behaviour: (a) partial grooming reconstruction of *Olenoides serratus*; (b) partial grooming reconstruction of *Triarthrus eatoni*. The fouling materials are reconstructed as randomly distributed irregular yellow shapes.

4.c. Other aspects of grooming

Folding or complex patterns of overlap among gill filaments have been recorded among early arthropods (Stein, 2013), and, if this also happened in live trilobites, grooming may also have helped in preening the gill filaments into optimal disposition, reducing the possibility of entanglement among the filaments of adjacent gill branches. If, as in modern arthropods such as horseshoe crabs (Sekiguchi *et al.* 1988), moulting frequency declined with age, grooming maintenance may have had an especially high premium at later ontogenetic stages, such as those preserved in the two cases discussed herein.

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