Omnidens appendages and the origin of radiodont mouthparts

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Running head: Omnidens assemblages from Xiaoshiba

Abstract

The sophisticated, modular and adaptable body plan of arthropods underpins their dominance in marine invertebrate communities. The origin of this body plan from legged lobopodian worms can be inferred from Cambrian Konservat-Lagerstätten, but our understanding retains some notable gaps: not least in the transition from swimming lobopodians such as *Kerygmachela* and *Pambdelurion* to robustly sclerotized radiodonts such as *Anomalocaris*. A large *Pambdelurion*-like fossil from the Xiaoshiba biota, *Omnidens qiongqii* sp. nov, exhibits a novel combination of characters: an oral apparatus with a non-radial configuration; and centimetric talon-like grasping structures with heavily sclerotized blade-like spines. The novel morphology broadens the interpretative framework for associated Cambrian taxa, demonstrating continuity in the morphology of euarthropod appendages prior to the origin of podomeres. A reappraisal of the euarthropod stem lineage suggests that radially arranged mouthparts may be a radiodont novelty, rather than an inheritance from the ancestral ecdysozoan. These results further resolve the evolutionary origins of the euarthropod body plan.

Introduction

Omnidens is known from assemblages of toothed plates in the Chengjiang biota, an early Cambrian site of exceptional fossil preservation (Chen *et al.* 1994; Gabbott *et al.* 2004; Hou *et al.* 2006, 2017*a*). The specimens are commensurate with a meter-long organism, which would be among the largest Cambrian predators. However, the isolation of the mouth apparatus from any associated body fragments – which is typical of large Cambrian fossils (e.g. Daley *et al.* 2009) – has left its affinity in question.

Omnidens was first interpreted as part of an anomalocaridid (lower stem-group Euarthropoda) mouth apparatus (Chen *et al.* 1994). However, prominent differences with known anomalocaridid mouthparts were argued to undermine this interpretation; a worm-like habit was proposed instead (Hou *et al.* 2006, 2017*b*). Subsequent work has increased the known disparity of mouthparts in anomalocaridids and other radiodonts (Daley *et al.* 2009; Daley & Bergström 2012; Cong *et al.* 2016, 2017), and has revealed the gradualistic nature of the transition from worm via lobopodian to anomalocaridid (Budd 1998*a*; Dzik 2011; Ortega-Hernández 2016; Smith *et al.* 2024). Specifically, the mouths of cycloneuralian worms and anomalocaridids are now interpreted as members of an evolutionary continuum, as indicated by the tooth-like pharyngeal elements in certain anomalocaridids and lobopodians (Daley *et al.* 2009; Vannier *et al.* 2014; Smith & Caron 2015; Vinther *et al.* 2016), and the potential homology between the toughened circumoral elements of anomalocaridids, lobopodians, and cycloneuralian worms

(Smith & Caron 2015). Indeed, the *Omnidens* tooth apparatus has been shown to exhibit such prominent similarity with the mouth of the gilled lobopodian *Pambdelurion* (Vinther *et al.* 2016) that the two taxa are conceivably synonymous.

Pambdelurion occupies a key position in the evolutionary history of euarthropods, denoting the transition from benthic lobopodian worms to free-swimming predators, close to the origin of the radiodont body organizational grade that straddles the euarthropod stem lineage (Zeng *et al.* 2020). *Omnidens* thus offers an opportunity to illuminate this formative period in the stepwise assembly of the euarthropod body plan.

Material and Methods

18 articulated specimens, and 26 slabs containing one or more disarticulated elements (Table 1), were collected from the Cambrian Stage 3 Hongjingshao Formation at the Xiaoshiba section in eastern Kunming, South China (Hou *et al.* 2019). Specimens occur alongside the candidate index trilobite *Hongshiyanaspis yiliangensis*, denoting a slightly younger age than previously described material (Hou *et al.* 2006) from Chengjiang (*Eoredlichia–Wutingaspis* zone). Specimens were prepared by manual removal of overlying matrix and photographed using a Leica M205-C stereomicroscope mounted with a Leica DFC 500 digital camera, and a Leica M205 FA fluorescence stereomicroscope with a Leica DFC7000 T monochrome digital camera. Fossils are deposited at the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming (YKLP).

Systematic Palaeontology

Stem group to Phylum EUARTHROPODA, Lankester, 1904

Genus OMNIDENS Hou, Bergström and Yang, 2006

Type species. *Omnidens amplus* Hou, Bergström and Yang, 2006; from the Chengjiang Biota, China.

Revised diagnosis

Oral apparatus comprising two symmetrically opposed crescents of plates and two talon-like structures. Each crescent comprises at least six principal plates, at least two accessory plates, and several rows of inner plates. Principal plates decrease in size from the middle of the crescent to each end; each exhibits an elongate trapezoid base and a single, slightly curved centripetal spine. Accessory plates have an oval base and bear one or more rows of conical spiny nodes. Inner plates are aligned with principal plates; they have oval bases that exhibit multiple elongate sub-conical spines. Plates in each subsequent row are smaller, and exhibit more spines: the first row of inner plates bears at least three spines, the second row of plates at least four, and subsequent plates at least five. The talon-like structures comprise a basal region whose proximal margin exhibits eight to ten robust, transversely flattened spines; spines are distributed symmetrically, decreasing in size from the middle towards each end.

Remarks

The initial diagnosis of *Omnidens* (Hou et al. 2006) conceived the crescents of plates as representing scalids and pharyngeal teeth of a priapulan worm, a concept that was overturned by comparison with the *Pambdelurion* oral cone (Vinther et al. 2016). The talon-like structures, originally described as *Amplectobelua* limb endites, have no counterpart in *Pambdelurion*; they are clearly not equivalent to the spinose elements of the *Pambdelurion* frontal appendages (Budd 1998*b*), nor to its cephalic spines (‘paired projections’) (Ortega-Hernández & Budd 2016; Young & Vinther 2017). The presence of talon-like structures in *Omnidens* supplement details in the configuration of the plates to justify the retention of *Pambdelurion* and *Omnidens* as separate, if closely related, genera.

Detailed comparison with *Pambdelurion* must contend with the different preservational style in Sirius Passet (Topper *et al.* 2018; Nielsen *et al.* 2021), where a higher degree of metamorphosis and volatilization has resulted in greater compaction than Chengjiang or Xiaoshiba, and has rendered the original carbon film more difficult to discern. The triangular appearance of the principal plates in *Pambdelurion* may reflect compression of *Omnidens*-like plates, and the concomitant adpression of the spine onto a trapezoid base. The limited preservational fidelity of the inner plates (pharyngeal teeth) of *Pambdelurion* does not reveal meaningful differences from those of *Omnidens*.

Modest differences are manifest in the accessory plates of *Pambdelurion*, whose two rows of papillae are inflected into chevrons, and whose papillae each bear a distinct central cusp; more prominently, *Pambdelurion* exhibits a larger number of accessory plates than have been observed in (admittedly incomplete) *Omnidens* assemblages, and accessory plates in *Pambdelurion* approach 65% of the area of principal plates (see figs. 1A–B, 3A, 4C–D in Vinther et al. 2016), compared with a much smaller ratio in *Omnidens*.

The plate series in *Pambdelurion* have been interpreted as exhibiting a radial arrangement, by comparison with radiodonts and priapulans (Vinther *et al.* 2016). However, the fossils themselves are consistent with a paired series of principal and inner plates, as in the *Omnidens* apparatus; whilst the accessory plates occur on a separate region of the fossils anterior and ventral to the oral apparatus.

Omnidens amplus Hou, Bergström and Yang, 2006

Revised diagnosis

Lateralmost principal plates lack accessory spines. Accessory plates with high density of nodes of mixed sizes, total exceeding twelve per plate. Inner plates form prominent columns, aligned with principal plates. First row of inner plates with four to five spines; second row with at least five spines; third row with at least six spines. Spines on inner plates closely adjacent and similar in size. Talon-like structures typically exhibiting eight spines.

Omnidens qiongqii sp. nov.

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Figures 1–6

2006 *Omnidens amplus* Hou et al. 2006, fig. 3b, ?3d, ?4c

2022 *Omnidens amplus*; Ou et al., 2022, fig. 4b

Etymology

qiongqii, pinyin 穷奇 (qióng qí), from the pre-Qin ancient book 山海经 (*the Classic of Mountains and Rivers*), is one of the four fierce beasts in ancient Chinese mythology. Its sharp teeth and greedy nature are consistent with the image of the species.

Type material

Holotype: YKLP 12460 (Fig. 1A); other referred material: YKLP 12461–12472, 12474–12475, 12477, and 12479–12481.

Locality and stratigraphy

Specimens were collected from mudstones of the Cambrian Series 2, Stage 3 Hongjingshao Formation at the Xiaoshiba section in eastern Kunming, Yunnan province, South China. They occur within the *Yunnanocephalus–Chengjiangaspis–Hongshiyanaspis* trilobite zone of the latest Chiungchussian Stage, corresponding to the lower biozone of Xiaoshiba Biota (Hou et al., 2019).

Diagnosis

Six principal plates, fourth narrower than second and fifth; first and sixth with two small accessory spines. Accessory plates with one or two rows of similarly sized nodes. Inner plates with at most five spines, each slightly separated from its neighbours; size of spines increases notably towards midline. Talon-like structures typically exhibiting ten spines.

Remarks

O. amplus is distinguished from *O. qiongqii* sp. nov. by its larger number of principal plates (at least seven), the uniform size of these plates (see fig. 4F in Zhang et al. 2014 and fig. 17.15 in Hou et al. 2017b); and the strict alignment of inner plates with principal plates. The number of spines and nodes on each inner and accessory plate is also higher in *O. amplus* (see figs. 489–490 in Chen 2004, figs. 4A, E, 5A–B in Hou et al. 2006 and fig. 4F in Zhang et al. 2014). Whilst the two morphotypes co-occur in Chengjiang, *O. amplus* has not been observed in more than 200 specimens from Xiaoshiba, suggesting that these differences are unlikely to represent intraspecific variation.

Description

The oral apparatus of *O. qiongqii* comprises two opposed series of trapezoidal plates, each with a single robust spine on its inner face (Figs. 1–2, 3A–D). The six principal plates (pp) of each series decrease in size in each direction away from the third plate (pp3), except pp4, which is narrower than pp2 and pp5. pp3 measures about 6.2 mm × 4.1 mm, with a spine 2.6 × 1.8 mm, in the smallest available specimen, and 38 × 14 mm (spine: 16 × 8.5 mm) in the largest; the smallest plates measure 4 × 3 mm (spine: 1.8 × 1.4 mm) in the smallest specimen, and 18.6 × 8.7 mm (spine: 8 × 6 mm, preserved laterally) in the largest. Individual plates are elongate trapezoids; the rounded peripheral face is wider than the central face. The peripheral edge of the plate series forms a curved arch, while the central faces align to provide a planar surface of opposition that would meet the adjacent plate series when the mouth was closed. Each spine is slightly curved, with a prominent keel; they are subtriangular in cross-section, with thick walls surrounding a central cavity, and the bottom significantly thicker (Figs. 2E, J); the dark colour of the walls denotes heavy sclerotization. Spines are around four times taller than wide, and three times longer than tall, and thus extend beyond the central face of each plate. Smaller accessory spines flank the main spine on the distalmost plates (Figs. 1C, 2A, F–H, 4A, C, 5C).

The accessory plates are rounded, measure 6.5 mm in diameter, and bear one (Fig. 4D) to two (Figs. 3A–B, 4A–C) series of small papillae (0.8–1.2 mm diameter). The construction of these papillae resembles that of the spines of the principal and inner plates, but they exhibit an oval cross-section, and do not extend beyond the faces of the plate. The accessory plates occur on a higher plane within the sediment than the principal plates (Figs. 2A, I, 3A–B, D, 5C) accounting for their inconsistent preservation; their position relative to the mouth apparatus thus reflects the angle of burial and the degree of deformation of the intervening soft tissue (Figs. 3C).

Each principal plate heads an inner series of at least three multicuspate oval plates, which get successively smaller into the pharynx (Figs. 1C, 2A, C–D, I, 3A–D). The inner plates are approximately equidimensional in plan view, though rows further into the pharynx are often preserved at a more oblique angle to the bedding surface, thus appearing foreshortened (Figs, 2C, 3A–B, D). Constriction of the pharynx causes the plates to meet along a single planar surface. As with the principal plates, the inner plates exhibit robust spines on their surface which point down the pharynx. The outermost plates bear three spines (Figs. 3E–H), subsequent plates four (Figs. 3I–L), and subsequent plates five (Figs. 3M–P).

One or two opposed pairs of bipartite talon-like structures (Figs. 1, 5C–D, Table 1) occur 5 to 38 mm from the oral apparatus. Equivalent structures associated with the type material of *O. amplus* were previously attributed to the chance superposition of *Amplectobelua* endites (Hou *et al.* 2006). Talon-like structures occur in five (Fig. 1B–C, 5C, 6D, G) of our 18 articulated specimens and 26 slabs, with the spinose face consistently directed towards the oral apparatus (e.g. Figs. 1, 6E). This is compatible with the structures being preserved (broadly) in life position and directing food to the mouth, and supports a biological relationship between the talon-like structures and the oral plates.

Each talon-like structure comprises two symmetrical components fused along a narrow depression at the midline. Each component comprises a base, measuring about 20–34 mm wide by 16–36 mm long; and five spines, which decrease in length from 27 mm adjacent to the midline (mode; range = 22–34 mm, N = 37) to 4 mm at the margins of the structure (range: 3–6 mm). Each spine is perpendicular to the base, curving gently and tapering to an acute point. The spines are often rotated to lie flat on the bedding surface, but have a very narrow, wedge-shaped cross-section, widest on the convex edge and tapering towards the concave surface (Figs.

1B–C, E, 6A–B, D–G). A medial ridge (Figs. 1B, E, 6D–E, G) and thickened concave surface (Fig. 1C, 6E–F, H–K) reinforce each spine. The cuticle of the spines is constituted of ribbon-like fibres that divide and merge (Fig. 6F–I); individual fibrils align with the spine (Fig. 6H, L–M). Flat, oval structures that resemble disarticulated carapaces of hymenocarine bivalved euarthropods occur alongside separate talon-like structures and oral apparatus (Fig.1A, 5A–B). Finally, a single specimen preserves one half of an oral apparatus and a single talon-like structure alongside a field of cuticular elements (Fig. 5C–D), a subset of which are flexible 'combs' measuring 1.25 to 2.57 mm wide and at least 10.2 mm long. These 'combs' comprise flexible carbonized lines that emerge at regular 0.26–0.31 mm intervals from a single basal rod that is 0.56–0.74 mm wide. The disposition of the combs can be explained by slight taphonomic distortion of an originally regular array of adjacent, serially repeated structures.

Interpretation

In view of the structural correspondence with the *Pambdelurion* mouthparts, *Omnidens* is best regarded as a gilled lobopodian with robustly sclerotized spine-bearing structures, representing a morphological intermediate between lobopod-bearing *Pambdelurion* and radiodonts closer to the euarthropod crown group, with sclerotized appendages (Fig. 7).

The hymenocarine-like carapaces conceivably represent sclerites of the *Omnidens* head, by comparison with early euarthropods (Ortega-Hernández 2015), and specifically the P-elements in *Amplectobelua* (Cong *et al.* 2017). The studied assemblages did not contain any components that obviously correspond to medial head sclerites.

We interpret the lineated cuticular bars (Fig. 5C–D) as setal blades, gill-like respiratory structures associated with radiodonts' flaps. In early-diverging euarthropods (*Kerygmachela*, *Pambdelurion*), labile wrinkle-like structures on the distal flaps (Budd 1993, 1998) are taken to correspond to the more clearly defined setal blades that are integrated with the flaps of e.g. *Opabinia* (Zhang & Briggs 2007) and *Innovatiocaris* (Zeng et al. 2022). In derived anomalocaridids such as *Aegiorcassis* (Van Roy et al. 2015) and *Hurdia* (Budd & Daley 2012), as with the *Omnidens* elements, setal blades often occur in isolation from the main carapace, and exhibit a perpendicular series of fine lamellae (0.55–4.8 per mm in *Aegirocassis*; 4–5.5 per mm in *Omnidens*).

Interpretation of the two talon-like structures is complicated by the potential for convergence. For example, similarities with the primary plates of the oral apparatus – bilateral symmetry; a hollow construction; a smooth base; concentric lines around the area where the spines are embedded in the bases; thickened spine bases with similar shape; and the size profile of spines – presumably reflect the application of a common genetic toolkit to similar functional constraints. We interpret the talon-like structures as forming a single left-right pair. Whilst comparison has previously been made with the gnathobase-like structures of *Amplectobelua* (Hou *et al.* 2006; Cong *et al.* 2017, 2018), the consistent presence of a single pair of talon-like structures suggests that the structures were not serially repeated, but formed a single pair. The length and sharpness of the spines and absence of a grinding base also suggests a grasping function not typical of gnathobases. A more pertinent point of comparison is with the distal components of the *Opabinia* and *Kerygmachela* frontal appendages (Whittington 1975; Park *et al.* 2018). These structures comprise a robust series of non-podomeric sclerotized spines that project anteriad from a common base, and which in *Opabinia* display an approximately bilateral arrangement (Whittington 1975 fig. 7).

Discussion

Omnidens exhibits the unexpected combination of a bilaterally arranged *Pambdelurion*-like oral apparatus with robustly sclerotized, but non-segmented, talon-like structures. A bilateral oral cone is surprising if we accept the continuity between the radial arrangement of the ancestral ecdysozoan mouthparts (Smith & Caron 2015; Vinther *et al.* 2016) and the tetraradial, or occasionally triradial, oral cones of radiodonts (Daley & Bergström 2012; Zeng *et al.* 2018). The oral cones of early euarthropods are typically reconstructed assuming a radial blueprint, which in many cases is compatible with, but not unambiguously demonstrated by, available fossil material. We contend that a bilateral, rather than radial, arrangement is consistent with the available fossil material for *Amplectobelua* (Cong *et al.* 2017), *Pambdelurion* (Vinther *et al.* 2016), *Jianshanopodia* (Vannier *et al.* 2014), *Lyrarapax* (Cong *et al.* 2014; Liu *et al.* 2018), and *Parapeytoia* (Budd 2021) (Fig. 7); in each case a conclusive characterization requires further material. This raises the question of whether the oral armature of euarthropods was necessarily radial. As onychophorans lack oral armature, and the homologies of radially arranged structures in tardigrades have been questioned (Kihm *et al.* 2023), the closest relatives of Euarthropoda do not conclusively inform the ancestral state – leaving open the possibility that euarthropod mouthparts were ancestrally bilateral in their arrangement (Fig. 7), and are thus not direct homologues of the circumoral spines in cycloneuralian ecdysozoans.

Phylogenetically, the presence of circumoral plates implies that *Omnidens* bore robust frontal appendages; these are presumably represented by the talon-like structures. Unlike the frontal appendages of radiodonts, these are not podomeric; a better comparison is with the frontal appendages of *Kerygmachela* (Park *et al.* 2018) or *Opabinia* (Whittington 1975), which bear robust claw-like spines that project distally from a non-sclerotized base. This points to a commonality of appendage construction in the deep region of the euarthropod stem lineage (Fig. 7), with these multiple spines potentially derived from the single claw that adorns the distal frontal appendage of lobopodians such as *Megadictyon* and *Jianshanopodia* (Vannier *et al.* 2014). Differentiation of the individual spines of the talon-like structures, in combination with increasing sclerotization of their bases, provides a plausible evolutionary pathway to the podomerically arranged spines of radiodont frontal appendages (Daley & Budd 2010). Of course, the recurrent evolutionary theme of morphological flexibility (Conway Morris 2022), exemplified in radiodonts (Lerosey-Aubril & Ortega-Hernández 2022), leaves open the possibility that the peculiarities of *Omnidens* are autapomorphic. But even then, *Omnidens* serves to increase the diversity of morphological form present at a key point in euarthropod evolution, where sclerotized components were becoming increasingly integral to the body plan. It helps to bridge the evolutionary gap between the 'soft-bodied' swimming lobopodians of the Sirius Passet environment and the radiodonts of Chengjiang and Xiaoshiba, whilst indicating that the development of a radiodont grade at the base of panarthropods was a decidedly non-linear process characterized by distinctive morphologies that were not retained by higher echelons of the euarthropod stem.

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DATA ARCHIVING STATEMENT

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Figure captions

FIG. 1. Articulated specimens showing the arrangement between the plates.

A, Holotype, YKLP 12460, showing two oral apparatus preserved with four talon-like structures and many carapace elements; B, YKLP 12464, showing right oral apparatus with a single talon-like structure; C–D, YKLP 12474 and interpretative drawing, showing oral apparatus with a single talon-like structure; E, YKLP 12466, showing a pair of talon-like structures with oral apparatus. *Abbreviations:* ca, carapaces; ccs, concave surface; cl, concentric lines; cvs, convex surface; dep, depression; ipr, inner plate row; lpp, left principal plates; lts, spine on left side of talon-like structure; oa, oral apparatus; rpp, right principal plates; rts, spine on right side of talon-like structure; sas, small accessory spine(s); tls, talon-like structure(s); tp, plate of talon-like structure. Scale bars represent: 10 mm (A, C–E); 5 mm (B).

FIG. 2. Oral apparatus: Principal plates.

A, YKLP 12475, close-up of Fig. 5A, showing a closed oral apparatus; B, Interpretative drawing of A; C, YKLP 12465, showing dorsal view of closed oral apparatus; D, close-up of Fig. 1E, showing dorsal view of oral apparatus; E, close-up of C, showing right principal plate bears a broken spine with thickened bottom; F–H close-up of D, showing lateralmost principal plates with small accessory spines at lateral sides; I, YKLP 12467, showing lateral and ventral preserved oral apparatus; J, close-up of (i), showing side-preserved principal plates. *Abbreviations:* ap, accessory plate; cl, concentric lines; lpp, left principal plates; pstb, thickened bottom of principal plates' spine; rpp, right principal plates; sas, small accessory spine(s). Scale bars represent: 10 mm (C); 5 mm (A, B, D, I); 2 mm (E, J); 1 mm (F–H).

FIG. 3. Inner series of plates.

A, oral apparatus with inner series of plates, see area boxed in Fig. 1A; B, YKLP 12461, counterpart of A, showing oral apparatus with inner series of plates; C, oral apparatus with inner series of plates, see area boxed in Fig. 1A; D, YKLP 12468, counterpart of Fig. 2I, showing oral apparatus with inner series of plates; E, inner plate of first row, dorsal view, see area boxed in Fig. 2C; F, close-up of D, inner plates of first row, anterior view; G, close-up of A, inner plates of first row, anterior view; H, inner plate of first row, lateral view, see area boxed in Fig. 1B; I –J, inner plates of second row, dorsal view, see area boxed in Fig. 2C; K, close-up of A, inner plates of second row, anterior view; L, inner plates of second row, lateral view, see area boxed in Fig. 1B; M, close-up of C, inner plates of the third row and subsequent, dorsal view; N, close-up of B, inner plates of the third row and subsequent, lateral view; O, inner plates of the third row and subsequent, anterior view, see area boxed in Fig. 2C; P, close-up of D, inner plates of the third row and subsequent, dorsal view. *Abbreviations:* ap, accessory plate; cl, concentric lines; lpp, left principal plates; rpp, right principal plates; sas, small accessory spine(s); tls, talon-like structure(s). Scale bars represent: 5 mm 5 mm (A–D); 2 mm (E, F); 1 mm (G–P).

FIG. 4. Accessory plates.

A, close-up of Fig. 3C, showing accessory plates with two rows of nodes; B, close-up of Fig. 3D, showing accessory plates with two rows of nodes; C, YKLP 12462, showing accessory plates with two rows of nodes; D, close-up of Fig. 2A, showing accessory plate with one row of nodes; E, reconstruction of original form of accessory plate. *Abbreviation:* cl, concentric lines. Scale bars represent: 2 mm (A); 1 mm (B–D).

FIG. 5. Associated cuticular elements.

A, YKLP 12475, showing oral apparatus preserved with carapaces and other species; B, YKLP 12471, showing TLS preserved with carapaces; C and D paratype, YKLP 12480 and 12481, showing numerous cuticular fragments surrounding the TLS and oral apparatus; E, close-up of C, fluorescence stereomicrographs showing arrangements and details of lineated cuticular bars; F, close-up of C, showing details of single lineated cuticular bar; G, close-up of D, showing arrangements and details of lineated cuticular bars. Abbreviations: bp, brachiopod pedicle; br, brachiopod; ca, carapaces; lpp, left principal plates; rpp, right principal plates; sas, small accessory spine(s); tr, trilobite; ts, TLS spine. Scale bars represent: 20 mm (A ⁻ D); 2 mm (E ⁻ G).

FIG. 6. Talon-like structures.

A, YKLP 12469, showing expansion of the TLS; B, YKLP 12470, counterpart of A, showing expansion of the TLS; C, reconstruction of talon-like structures from convex and concave sides; D, YKLP 12463, showing transverse expansion of the TLS; E, close-up of Fig. 6B, showing a pair of crossed TLS; F, YKLP 12477, showing single TLS with two types of longitudinal ribbon-like fibres on spine; G, YKLP 12479, showing single TLS with two types of longitudinal ribbon-like fibres on spine; H–I, close-up of (g), showing two types of longitudinal ribbon-like fibres on lateral preserved TLS spine; J–K, close-up G, showing ventral and lateral preserved TLS spines with thickened bottom and base opening; L–M, YKLP 12472, fluorescence stereomicrographs showing longitudinal ribbon-like fibres on spine ridge; N, reconstructed shape and structure of spines in talon-like structures. *Abbreviations:* bo, base opening; cv, cavity; dep, depression; rlf, ribbon-like fibres; tp, plate of TLS; ts, TLS spine; tsr, ridge of TLS spine; tstb, thickened bottom of

TLS spine. Scale bars represent: 10 mm (A, B, D, E); 5 mm (F, G); 2 mm (H, I); 1 mm (J, K); 0.5 mm (L, M).

FIG. 7. Origins of euarthropod appendages and mouthparts.

Phylogenetic model (after Pates *et al.* 2022) showing interpreted position of *Omnidens* within euarthropod stem lineage. Schematics depict frontal appendages, interpreted assuming homology of terminal spines; and arrangement of oral armature, assuming early origin of bilateral arrangement. Schematics are drawn with reference to: *Jianshanopodia*, Early Life Institute (Xi'An) J001 (Vannier *et al.* 2014); *Kerygmachela*, MGUH (Geological Museum, Natural History Museum of Denmark) 32054 (Park *et al.* 2018); *Pambdelurion*, MGUH 24508, 30506, 31553, 31554 (Budd 1998*b*; Vinther *et al.* 2016); *Opabinia*, Smithsonian National Museum for Natural History 57683, 155600 (Whittington 1975; Pates *et al.* 2022); *Hurdia* (Radiodonta), Royal Ontario Museum 59257, 60026 (Daley *et al.* 2013).

Table 1. Composition of examined material.

Part/counterpart pairs are denoted A/B. A single complete series of the oral apparatus comprises six principal plates and corresponding rows of inner plates. Measurements denote distances between each element and the closest oral apparatus. Abbreviations: AP, accessory plate(s); TLS, talon-like structure(s).

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