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**THE MOUTH APPARATUS OF THE CAMBRIAN GILLED LOBOPODIAN
*PAMBDELURION WHITTINGTONI***

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Abstract: *Omnidens* is a large feeding apparatus composed of circlets of teeth, first documented from the early Cambrian of China. Originally interpreted as the oral cone of a radiodontan, it was later reinterpreted as the introvert of a priapulid. In both cases the *Omnidens* mouthparts underpinned estimates of gigantic (ca 2 metres) body size. Recent evidence has been used to suggest that pharyngeal teeth and radially-arranged oral plates in the stem-group onychophoran *Hallucigenia* and the lower stem-group euarthropod *Jianshanopodia* are homologous to structures of the introvert in priapulids and other scolidophorans, and are thus primitive characters for moulting animals (Ecdysozoa) as a whole. Here we show that the early Cambrian gilled lobopodian *Pambdelurion whittingtoni* from Sirius Passet, Greenland, possesses a mouth apparatus identical to *Omnidens*, being composed of the same three zones with detailed similarities of sclerites in each zone. An oral cone with rings of pharyngeal teeth, radial plates, and outer scolid-like plates are ecdysozoan characters retained in the euarthropod stem group. *Omnidens* from China likely belongs to an unrecognised *Pambdelurion*-like animal rather than being part of a giant priapulid.

Keywords: Cambrian, *Pambdelurion*, Sirius Passet Lagerstätte, Ecdysozoa,

CONSIDERATION of the affinities of radiodontans such as *Anomalocaris* and allied Cambrian animals such as gilled lobopodians has drawn heavily on the anatomy of the mouth apparatus. Morphological knowledge of Radiodonta was fundamentally illuminated by complete specimens from the Burgess Shale in Canada and the Chengjiang Biota in China. Chengjiang radiodontans came to light with the documentation of new taxa and anatomical structures in the 1990s (Chen *et al.* 1994; Hou *et al.* 1995), prompting hypotheses about evolutionary relationships to other giant predators of the Cambrian, and opening up a controversy over whether these animals are stem-group euarthropods (Budd 1997, 1999) or more closely related to cycloneuralian worms such as priapulans and nematodes (Hou *et al.* 1995). A position on the euarthropod stem group has since gained further support (Daley *et al.* 2009; Smith and Ortega-Hernández 2014), and radiodontans are now interpreted as apex predators of the Early Palaeozoic (Daley *et al.* 2013; Vinther *et al.* 2014; Van Roy *et al.* 2015). They possess a mouth apparatus composed of radial plates of different sizes and shapes, originally described as a separate entity in the Burgess Shale (*Peytoia*) (Whittington and Briggs 1985).

Associated with Chengjiang specimens are large tooth plates, which were interpreted as being part of the radiodontan *Amplectobelua* Hou *et al.* 1995. The size of these oral elements prompted an estimate of a >2 metre body length, greater than any estimates based on frontal appendages (Chen *et al.* 1994). However, a radiodontan identity for the mouth plates was subsequently rejected and they were reinterpreted as parts of the introvert of a large priapulan, named *Omnidens amplus* (Hou *et al.* 2006). Similarly, the large tooth plates prompted a reconstruction of *O. amplus* as the largest known priapulan in history.

Recent discoveries have demonstrated the presence of pharyngeal teeth and radially-arranged circumoral plates in the lower stem-group euarthropod *Jianshanopodia* (Liu *et al.* 2004; Vannier *et al.* 2014) and the stem-group onychophoran *Hallucigenia* (Smith and Caron 2015). These have been homologised with elements of the introvert of scalidophorans and nematoids,

and homologues of these have been proposed in extant Tardigrada and Euarthropoda (Smith and Caron 2015). This distribution suggests that the stem lineages of the three panarthropod phyla (tardigrades, onychophorans and euarthropods) retained modified oral cones inherited from the common ancestor of Ecdysozoa (Dewel and Dewel 1997; Smith and Caron 2015).

Here we demonstrate that the lower stem-group euarthropod (*sensu* Ortega-Hernández 2016) *Pambdelurion whittingtoni* Budd, 1997 from the Sirius Passet Konservat-Lagerstätte in North Greenland (Budd 1997) possesses an *Omnidens* mouth apparatus (Figs. 1, 2). This contradicts a priapulid identity for *Omnidens* mouthparts in China and instead supports a stem-group euarthropod identity for these intriguing fossils. Implications for homologies of mouthparts in Panarthropoda are considered in light of these new findings.

MATERIAL AND METHODS

Several hundred specimens of *Pambdelurion whittingtoni* have been collected from Sirius Passet (Conway Morris *et al.* 1987; Ineson and Peel 2011), sourced from both talus and outcrop. All specimens are preserved in dorsoventral aspect, and due to their large size, most are incomplete. Four specimens preserve the mouth apparatus in reasonable detail, one of them associated with very large button-shaped sclerites. They are housed in the Natural History Museum of Denmark (prefix MGUH). The oral cone was originally recognised as a “Peytoia” mouthpart (Budd 1997), but other than being radial and situated ventrally in the head, anatomical details were ambiguous.

Specimens were photographed in low angle lighting, coated with magnesium oxide smoke or ammonium chloride sublimate. Some specimens were also photographed at various angles for post-processing via polynomial texture mapping (Hammer and Spocova 2013). Reflective Transformation Imaging (Malzbender *et al.* 2001) used the Hemispherical Harmonic algorithm (Wang *et al.* 2009) in FTIBuilder v. 2.02. Specimens collected *in situ* preserve features visible as reflective films (Vinther *et al.* 2011a, b; Vinther *et al.* 2014), which were visualised under water and high angle illumination. Interpretative

drawings were made by camera lucida or in Adobe Illustrator from photographic images.

To estimate maximum body size, complete specimens were measured for length and distance from the midline to the first trunk flap. Specimens preserving oral cones all lack the posterior end but preserve their lateral extent. Ratios between triangular plates and oval sclerites in the mouth apparatus in relation to body-width at the first trunk segment were measured and scaled to the relation of the body width and length in the largest complete specimen.

The phylogenetic context and taxonomic nomenclature used herein follow Ortega-Hernández (2016, fig. 2). *Jianshanapodia/Megadictyon*, *Kerygmachela*, *Pambdelurion*, *Opabinia* and *Radiodonta* are interpreted as a paraphyletic series on the euarthropod stem-lineage that is collectively grouped as lower stem-group Euarthropoda.

DESCRIPTION

The head of *Pambdelurion whittingtoni* has a rounded anterior margin that bears paired sets of three spine-like elements (Fig. 3A, B; Ortega-Hernández and Budd 2016), flanked by a pair of ventrolaterally attached, annulated frontal appendages, the latter equipped with paired spines along their inner margins.

The mouth apparatus is situated ventrally on the head in variable configurations relative to the anterior margin and frontal appendages. Different specimens (MGUH 24508, 30506) preserve the apparatus either in posteriorly- or anteriorly-facing lateral view, suggesting some degree of mobility from which we infer that the apparatus was accommodated on a mobile, protrusible cone. The apparatus consists of three distinct, radially arranged elements: 1) outer plates; 2) large triangular plates, forming a ring; 3) an inner array of small pectinate sclerites. The outer plates (Fig. 4E, F) are ovate or button shaped in outline. They are arranged radially around the mouth, but our specimens only preserve them along the anterior half of the mouth apparatus (Fig. 1). These plates bear tubercles and blunt cusps disposed in two parallel rows. The number of cusps seems to differ between specimens of different sizes. The triangular plates (Figs. 2A, B, 4C, D) contact each other at their bases, but some specimens

show some degree of overlap. We interpret the overlap as a taphonomic alteration because in those cases the tips of the plates do not point towards the centre of the mouth (Fig. 2B). The number of triangular plates in the ring cannot be counted with precision in any specimen (being consistently partly incomplete), but the most complete specimen has 13-14 definite plates (Fig. 2B). Extrapolating based on consistent size throughout the ring predicts a total of ca. 16 plates. The triangular plates have a median crest along the apical region that extends at least half the length of the plate (Fig. 4D). The inner sclerites (Figs. 2A, 4E, F) are poorly preserved but bear five or six spines, their apices directed towards the centre of the mouth apparatus. The precise number of whorls of inner sclerites is not discernible but there appear to be at least two. The outer oval plates are sometimes superimposed on the basal parts of the triangular plates (Figs. 3A, B, 4C, D), and are either concave and smooth or convex and tuberculate. It appears that these plates are embedded in an integument because they are occasionally superimposed on the basal part of the circlet of triangular plates, which in such specimens appears effaced, in contrast to the sharp margins of the distal parts of the triangular plates (Fig. 2A). The exceptional quality of preservation of these specimens, showing fine details of annulations on the frontal appendage and having a complete, arcuate anterior margin (Fig. 1, 2A) suggests a concealing integument over the mouth apparatus that bore these oval plates rather than displacement due to decay. The sclerite arrangement seen in SP-2009-0939 (Figs. 1A, B, 2A, 4C, D) is interpreted as the result of dorsoventral compaction of the extruded mouth cone. As the mouth bent on top of itself the oval plates of the posterior margin were flipped under the mouth cone, hence leading to variable preservation and relief (Fig. 3C).

DISCUSSION

The mouth cones of *Pambdelurion whittingtoni* and *Omnidens amplus* (Fig. 5) share the following characters that attest to their close affinities: 1) the outer part of the mouth apparatus bears ovate plates with radially arranged tubercles and cusps; 2) a single ring of large triangular plates (“very large spines” (Hou *et al.* 2006), each with a median crest-like apical spine; 3) the numbers of

triangular plates is apparently conserved (an estimated 14-16 in *Omnidens* matches that of *Pambdelurion*); 4) the inner part of the oral cone contains circlets of oval tooth plates that each bears a pectinate spine fringe. Large, denticulate sclerites associated with *Omnidens* (Hou *et al.* 2006, fig. 3E) are of uncertain identity and have been interpreted as parts of another organism, such as the radiodontan *Amplectobelua* (Hou *et al.* 2006). Although comparable sclerites have not been found in or near the mouth apparatus of *Pambdelurion*, comparison with the latter opens the possibility that they could be the distal part of the frontal appendage, which in some specimens is configured as a cluster of recurved spines (Fig. 1C, D; Vannier *et al.* 2014, fig. S2g).

The similarity in the relationships of the three main components of the oral region and the details of each component are so exact that the taxonomic distinction between *Pambdelurion* and *Omnidens* is open to question. Presently we defer formal synonymy of *Omnidens* in the absence of associated body parts in its type area, Chengjiang. The correspondence between *Pambdelurion* and *Omnidens* indicates that priapulid affinities for the latter are untenable, given that the whole-body morphology of *Pambdelurion* is known and is demonstrably that of a gilled lobopodian. *Pambdelurion* now provides a search image for the Chengjiang animal that bears the *Omnidens* mouthpart. Currently no gilled lobopodians are known from this biota and, based on size and phylogenetic proximity, the only plausible candidates are large-bodied lobopodians such as *Megadictyon cf. haikouensis* (Liu *et al.* 2007) and *Jianshanopodia decora* (Liu *et al.* 2006). The pharynx of *J. decora* bears circlets of teeth comparable to those of priapulids (Vannier *et al.* 2014). If such lobopodians are indeed the bearers of the *Omnidens* mouth apparatus, then the detailed similarity to *Pambdelurion* would imply a remarkable degree of conservatism in mouthparts in the lower euarthropod stem group.

A reassessment of body size as outlined in Material and Methods draws on the largest complete specimen of *Pambdelurion*, which is 46 cm in length. The largest individual skeletal element of *Omnidens* is a triangular plate of length 47 mm (Hou *et al.* 2006); an association of oval sclerites from *Pambdelurion* (Fig. 4A) of 8 mm is its largest mouthpart element. Comparison of the relationship of the body length to the size of the mouth apparatus leads to an estimate that

Pambdelurion could have grown to 55 cm in length, while *Omnidens* would have reached 1.5 metres. These estimates of *Omnidens* are larger than those for any Cambrian radiodontan, thus the *Pambdelurion/Omnidens*-grade lobopodians are likely to represent the largest vagile Cambrian organisms known.

Although no specimens of *Pambdelurion* preserve the mouth apparatus in side view, we interpret it as a muscular cone similar to that in some specimens of *Opabinia regalis* (Whittington 1975) based on the fact that the mouth cone can be preserved in different positions without post-mortem alteration, which points to a motile nature of the apparatus. Furthermore, some specimens preserve phosphatised muscles in the oral region that could potentially be homologised to the retractors and protractors of tardigrades and scalidophorans, further suggestive of the mouth having some degree of kinesis. From a functional point of view we envision the mouth of *Pambdelurion* as a structure similar to the eversible pharynx of priapulids and errant annelids. A proposed model for the sequence of eversion in *Pambdelurion* (Fig. 3D) draws on inferences from the phylogenetic bracket of extant ecdysozoans.

For some two decades, morphology of the mouthparts has been cited as depicting shared derived characters of Ecdysozoa, based on features shared by cycloneuralians, tardigrades and other panarthropods. Particular similarities include a mouth cone with radial or biradial symmetry (Dewell and Dewell 1997) and circumoral plates (Waggoner 1996). The discovery of a potentially protrusible, radial mouth cone and circlets of pharyngeal teeth in the gilled lobopodian *Pambdelurion* (Fig. 6) demonstrates that these characters are not exclusive to cycloneuralians and stem-group onychophorans (Smith and Caron 2015). Rather, as anticipated by *Jianshanopodia* (Vannier *et al.* 2014) and more clearly shown by the radial mouth cone of Radiodonta, these characters are present in the euarthropod stem-group as well (Budd 1998). This character distribution is consistent with radial circumoral plates and a protrusible pharynx bearing radially-arranged teeth being ground-pattern characters of Ecdysozoa. Similarity between the ovate sclerites of *Omnidens* and the scalids of priapulans was noted by Hou *et al.* (2006), and served as an argument for the proposed identity of that taxon as a priapulid. We reiterate this similarity, shared by the ovate sclerites of *Omnidens* as well, which includes their position and detailed

morphology (Fig. 2D for scalids of the extant *Priapulius caudatus*). Homology of scalids and the ovate plates of stem-group euarthropods would imply that scalids are not necessarily an autapomorphy of Scalidophora but may instead be a general character of Ecdysozoa, or a subgroup that includes scalidophorans and panarthropods.

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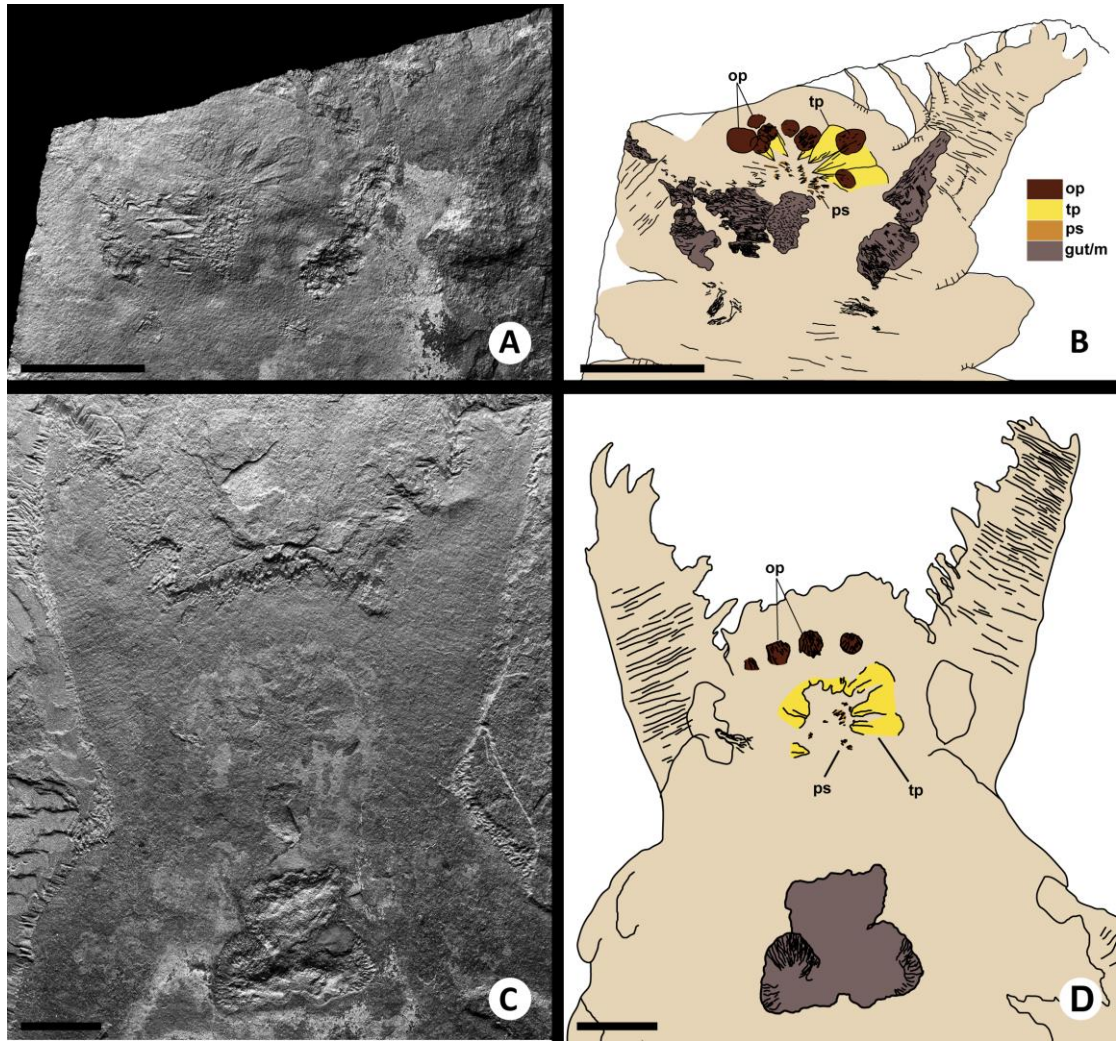


FIG 1. Mouth apparatus of *Pambdelurion whittingtoni*. A, B, head and first trunk segment, and detail of mouth apparatus, MGUH 31553. C, D, head and anterior part of trunk, MGUH 30506. Photos created using polynomial texture mapping. Abbreviations: gut/m, phosphatised gut and muscle tissue; op, oval plates; ps, pharyngeal spines; tp, triangular plates. Scale bars 20 mm.

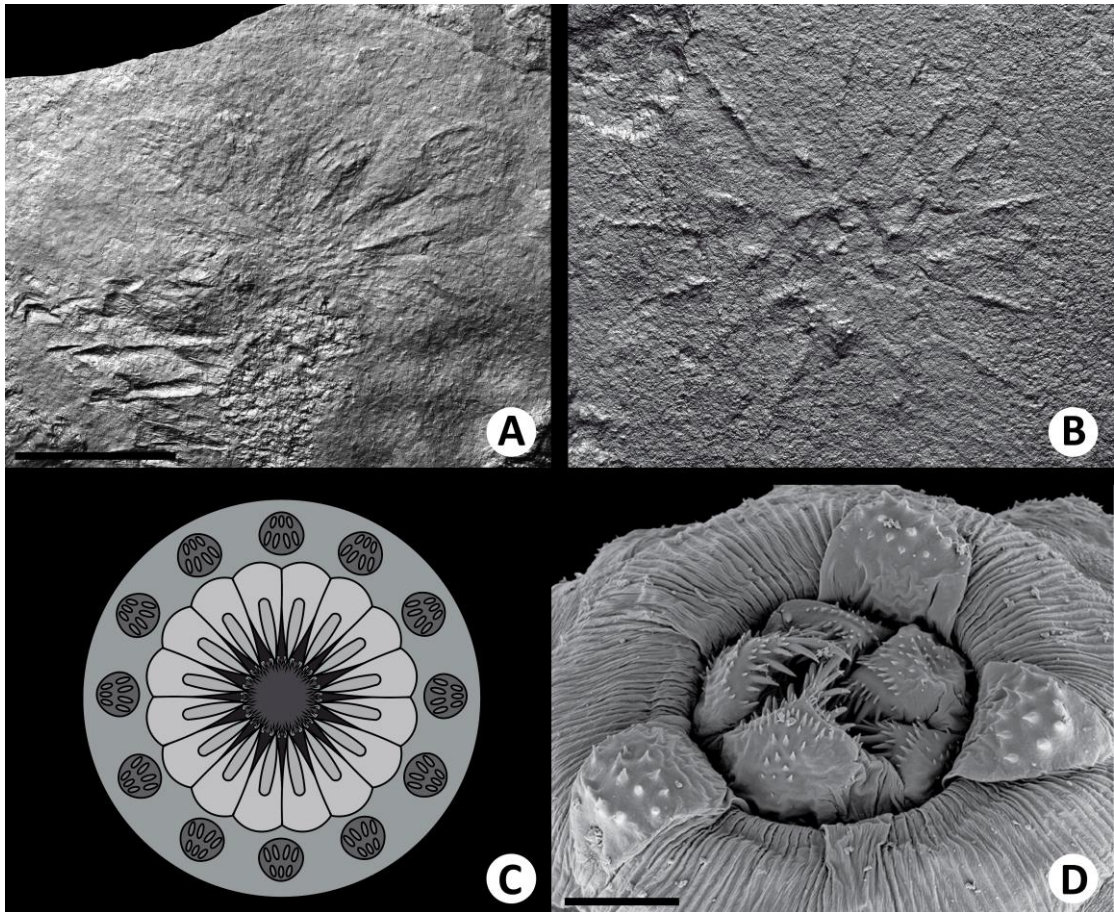


FIG 2. A-C, mouth apparatus of *Pambdelurion whittingtoni*. A, MGUH 31553, scale bar 10 mm. B, mouth apparatus, MGUH 31554. C, schematic representation of plate associations. D, *Priapulus caudatus*, second loricata larva with partly protruded mouth cone (from Wennberg *et al.* 2009).

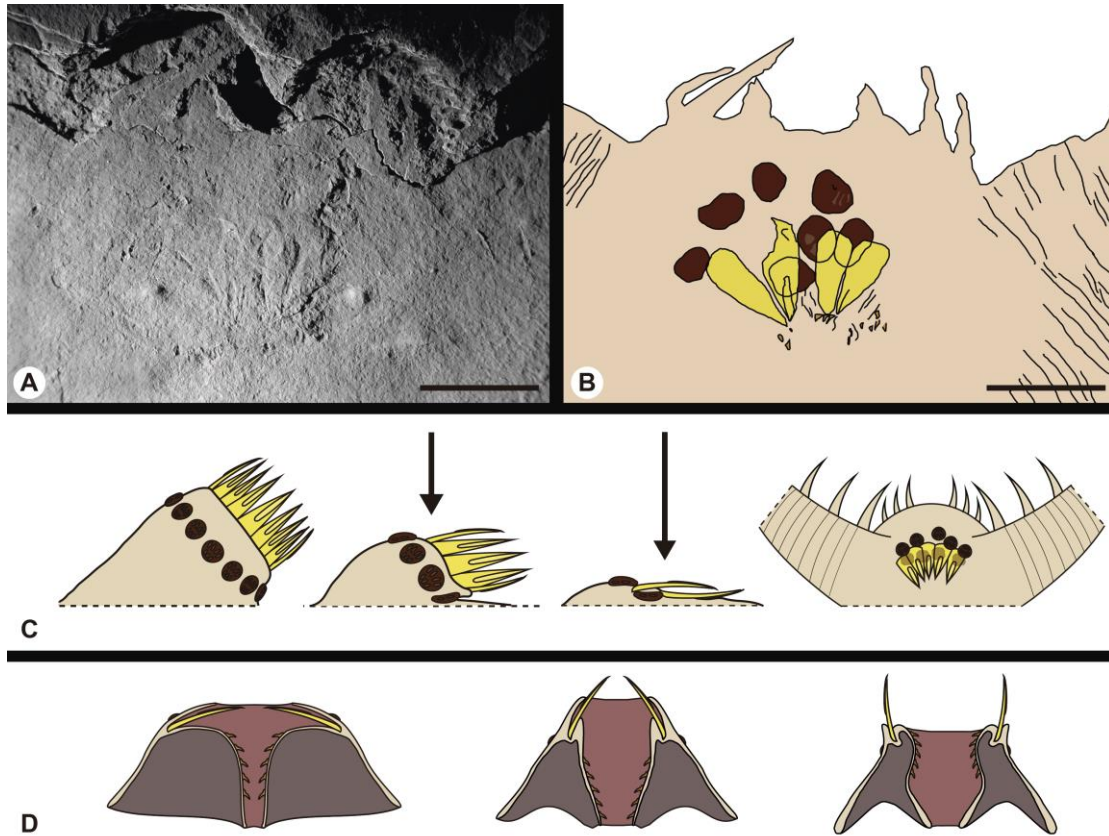


FIG 3. Mouth apparatus of *Pambdelurion whittingtoni*. A, B, holotype MGUH 24508, frontal region, preserving laterally compressed mouth apparatus, photographed with ammonium chloride sublimate. Scale bar 10 mm. C, schematics explaining mouth orientation. Oral cone everted and posteriorly projected when buried, compaction resulted in oval plates being superimposed by the oral cone with the inner, smooth surface exposed while oval plates on the exposed top surface show tubercles. D, sequence of eversion of mouth cone.

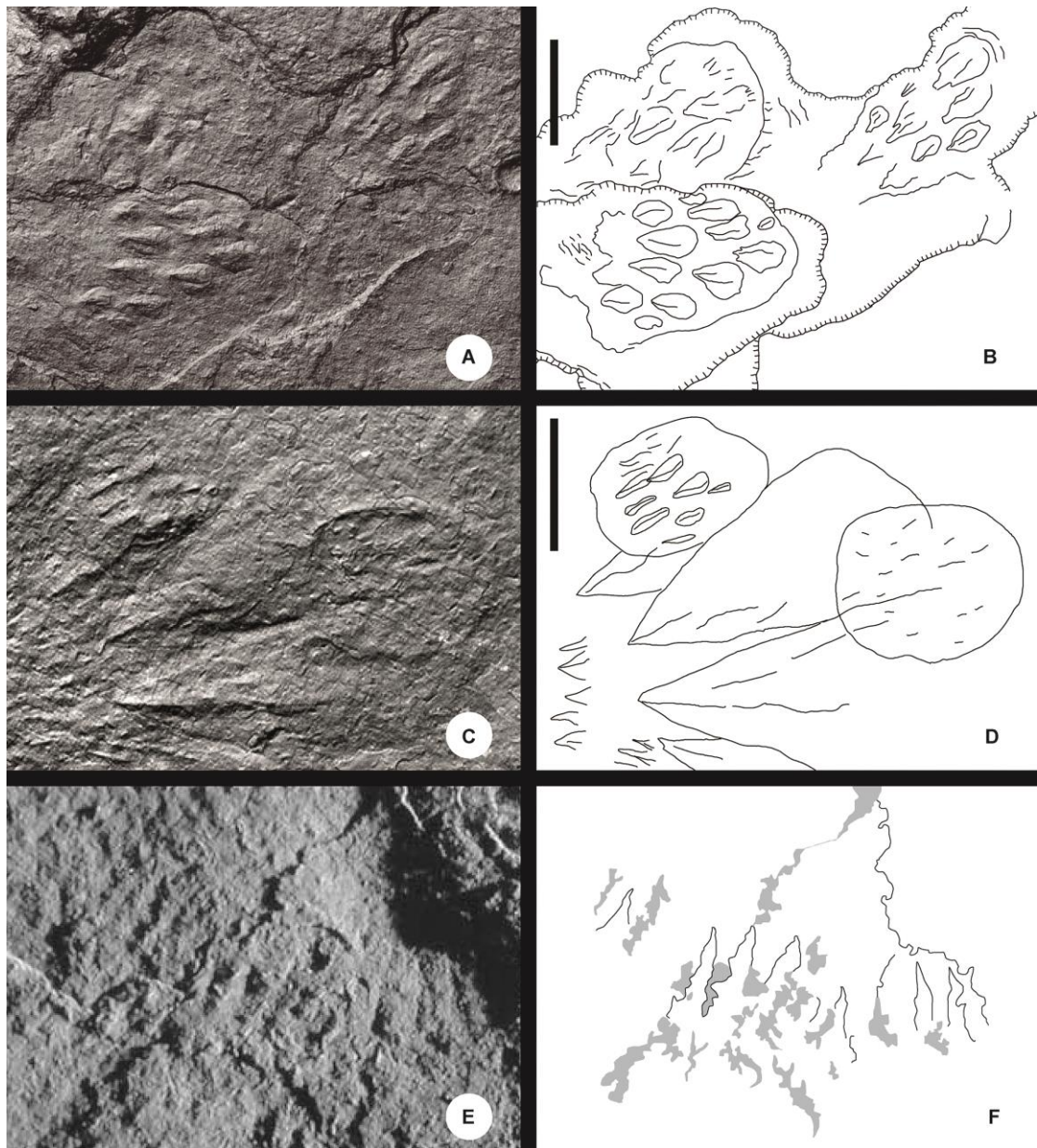


FIG. 4. Mouth apparatus of *Pambdelurion whittingtoni*. A, B, detail of oval plates, MGUH 31555. C, D, detail of triangular plates (note superimposed oval plates), MGUH 31553. E, F, detail of pharyngeal teeth, MGUH 24508. A, C, polynomial texture maps; E photographed with ammonium chloride sublimate. Scale bars 5 mm (A, B), 10 mm (C, D).

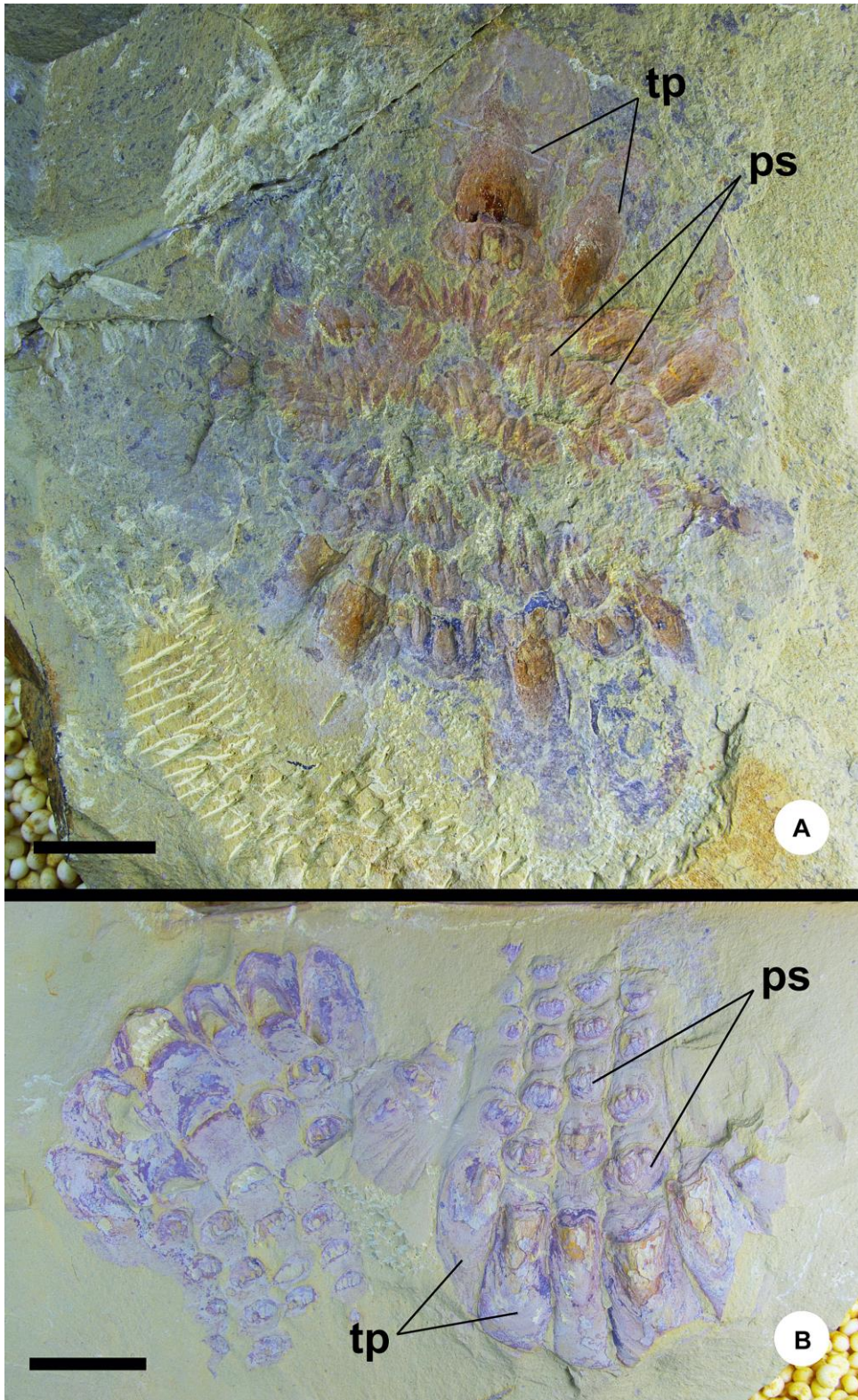


FIG. 5. Mouth apparatus of *Omnidens amplus* Hou *et al.*, 2006. A, YKLP 10157. B, YKLP 101053, 10154. Abbreviations: ps, pharyngeal sclerites; tp, triangular plates.

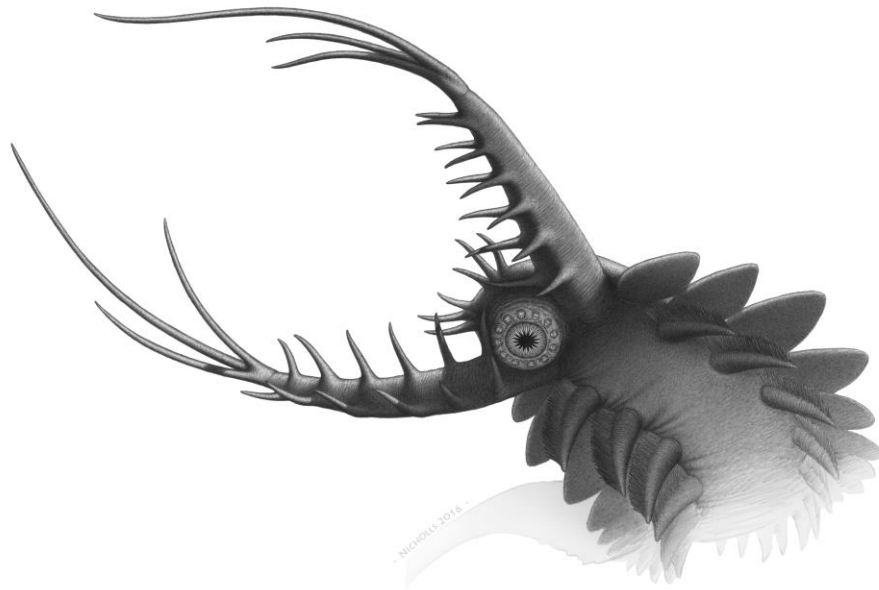


FIG 6. Reconstruction of head region of *Pambdelurion whittingtoni*. courtesy of Bob Nicholls, palaeocreations.com