The three-dimensionally articulated oral apparatus of a Devonian heterostracan sheds light on feeding in Palaeozoic jawless fishes

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ABSTRACT

Attempts to explain the origin and diversification of vertebrates have commonly invoked the evolution of feeding ecology, contrasting the passive suspension feeding of invertebrate chordate and larval lampreys with active predation in living jawed vertebrates. Of the extinct jawless vertebrates that phylogenetically intercalate these living groups, the feeding apparatus is preserved only in the early diverging stem-gnathostome heterostracans, and its anatomy remains poorly understood. Here we use X-ray microtomography to characterise the feeding apparatus of the pteraspid heterostracan *Rhinopteraspis dunensis* (Roemer, 1855). We show that the apparatus is comprised of thirteen plates arranged approximately bilaterally, the majority of which articulate from the postoral plate, except those close to the midline which are shorter and must have floated in soft tissue. Our reconstruction of the apparatus shows that these plates would have been capable of movement within the dorso-ventral plane, but this was likely limited. The functional morphology of the apparatus in *Rhinopteraspis* precludes all proposed interpretations of feeding except for suspension feeding and we interpret the apparatus as having served primarily to moderate the oral gape. This is consistent with evidence that at least some early jawless gnathostomes were suspension feeders, a proposition based previously only on disarticulated parts of the heterostracan oral apparatus, and runs contrary to ideas of the earliest vertebrates as predators. However, body shape and the position of the mouth varies considerably in heterostracans, and analyses based on individual pteraspid taxa may not capture the diversity of feeding in the group.

Keywords: Heterostracan, Pteraspid, Feeding, Devonian, Palaeozoic, Ostracoderm

1. Introduction

Feeding figures prominently in attempts to understand the evolutionary origins of vertebrates (Janvier 1996, Anderson *et al.* 2011). In contrast to invertebrate chordates, which exclusively suspension feed with either a ciliated pharynx or a mucus net (Hamann and Blanke 2022), the dorso-ventrally closing jaws of living vertebrates (in gnathostomes, jawed vertebrates) (Anderson and Westneat, 2007; DeLaurier, 2019; Smithwick, 2015) or antero-posteriorly moving system of cartilages (in cyclostomes, hagfishes and lampreys) (Clark and Summers, 2007; Clubb et al., 2019; Dawson, 1963; Hilliard et al., 1985) allow for a far broader range of feeding strategies. The evolution of these unique vertebrate feeding modes plays a major role in attempts to explain the origins of vertebrate anatomy and modern diversity (Mallatt 1984, 1996). Prominently, the New Head Hypothesis (Northcutt & Gans 1983, Gans & Northcutt 1983, Gans 1989, Gans, 1993, Northcutt 1996, Northcutt 2005) argues that the shift from suspension feeding to predation accompanied the emergence of neural crest, neurogenic placodes, and the accompanying evolution of a prechordal head. This hypothesis predicts that a predatory feeding mode existed in the earliest vertebrates with a prechordal head.

The fossil record of Palaeozoic vertebrates provides a means of testing whether this is the case, but is far from decisive. In particular, the heterostracans, an extinct group of jawless stem-gnathostomes, has been the focus of much of the debate over early vertebrate feeding. This is due to their oral region being typically the most completely preserved, and they are often interpreted as one of the earliest diverging lineages of stem-gnathostomes and, as such, have the potential to inform on the nature of the feeding ecology of the earliest members of the gnathostome lineage (Keating et al. 2018). The heterostracan feeding apparatus is best known in pteraspids, where the oral region is characterised by distinctive macromeric dermal plates (Blieck, 1984; Kiaer, 1928; Randle and Sansom, 2017; White, 1935). The function of these plates has been much debated, variously interpreted as biting (Kiaer, 1928) or slicing (Bendix-Almgreen 1986) ‘jaws’, a cyclostome-like feeding apparatus (Janvier, 1974; Jarvik, 1980; Stensiö, 1958, Stensiö, 1958), a sediment scoop (White, 1935), or a filtering structure (Janvier, 2015; Lingham-Soliar, 2014; Stiefel, 2021). Equally varied are the inferred ecologies, with heterostracans interpreted as active predators (Kiaer, 1928), macrophagous selective predators (Denison 1961; Northcutt and Gans 1983), hagfish-like scavengers (Janvier 1974; Jarvik 1980, Stensiö, 1958, Stensiö, 1958), herbivores (Bendix-Almgreen 1986), detritivores (White 1935; Dineley and Loeffler 1976), or suspension feeders (including filter feeding) (Halstead, 1973; Heinz, 1962; Mallatt, 1984; Mallatt, 1985; Purnell, 2002; Romer, 1959).

The difficulty in studying the articulated heterostracan oral apparatus *in situ* contributes to this lack of consensus. In rare cases where it is preserved, articulated heterostracan oral apparatuses consist of small plates suspended in encasing sediment. As a result, previous reconstructions of the oral apparatus have focused either on the gross arrangement of the apparatus, in which the morphology and detailed arrangement of the individual plates is not addressed (Janvier, 1974; Stensiö, 1964, 1958; White, 1935), or describe isolated elements with little or no reference to articulated apparatuses (White 1935, 1961; Ball and Dineley 1961). The most recent investigation suggests that heterostracans were suspension feeders because the analysed oral plates exhibited no evidence of the wear anticipated of a tooth-like function (Purnell 2002).

Evidently, the feeding ecology of heterostracans remains in its infancy and we seek to advance understanding through a detailed characterization and reconstruction of the heterostracan oral apparatus. We used X-Ray microtomography to characterise the three-dimensionally (3D) articulated oral apparatus in an exceptionally well-preserved specimen of the pteraspid heterostracan *Rhinopteraspis dunensis* (Roemer, 1855). Using computed tomography, we generate 3D models of the components of this apparatus and use this to build a detailed three-dimensional reconstruction and description of the articulated mouthparts of a pteraspid heterostracan. We use this reconstruction to assess competing hypotheses of heterostracan feeding.

2. Materials & Methods

(a) Specimens and locality

Rhinopteraspis dunensis (Roemer, 1855) NHMUK PV P 73217 is housed in the collections of the Natural History Museum, London (NHMUK). In the museum catalogue the specimen is listed as being collected from “Odenspiel Quarry”, likely corresponding to Jaeger Steinbruch, a quarry near the village of Odenspiel, Reichshof, North-Rhine Westphalia, Germany or, possibly, to outcrops in the local area (Conzen and Gerlach, 1993; Hartkopf-Fröder et al., 2015). The Jaeger Quarry and surrounding outcrops expose sandstones and mudstones belonging to the Siegenian (?upper Pragian or lower Emsian, Lower Devonian) Odenspiel Formation (Becker et al., 2020, Poschmann *et al.* 2016), deposited on the northern margin of the Rhenohercynian Basin, which represents a marginal transgressive and regressive delta dominated setting (Stets and Schäfer, 2009). The Odenspiel Formation falls within the ‘Pararhenotypics subfacies’ of Jansen (2016), representing a marginal marine, intertidal lagoonal setting containing a restricted fauna of fish, bivalve molluscs, lingulid and terebratulid brachiopods, and eurypterids (Conzen and Gerlach, 1993; Hartkopf-Fröder et al., 2015; Hartkopf-Fröder and Weber, 2016; Schmidt, 1959; Weber and Hartkopf-Fröder, 2016).

(b) Terminology

Various different terminologies have been applied to different parts of the pteraspid oral region. In this study we preferentially follow the terminology used by Randle and Sansom (2016) and, where that is not possible, that of Blieck (1980).

(c) Computed tomography

Rhinopteraspis dunensis NHMUK PV P 73217 (Fig. 1) was scanned using a Nikon Metrology XTH 225ST X-ray tomography instrument based in Bristol Palaeobiology, University of Bristol. Two scans were undertaken, each composed of two stacked scans. The first scan set included the whole headshield at a voltage of 223 kV and a current of 193 µA, with 3141 projections, and with a 1 mm Sn filter, obtaining a dataset with 63.41 µm voxel resolution (Fig. 1). The second scan set targeted the oral region specifically, including the posterior third of the rostrum, the orbital, oral, and pineal parts of the headshield, and the anterior quarter of the dorsal and ventral discs, at a voltage of 180 kV and a current of 178 µA, with 3141 projections of 8 frames and 708 ms each, and with a 0.5 mm Cu filter, achieving a voxel resolution of 22.91 µm (Figs 2-4).

The tomographic datasets were segmented in Mimics v.25 (materialise) to create 3D models. All 3D models were visualised in Blender 3.5 (blender.org).

(d) Reconstruction and animation

3D models of the higher resolution scan set of *Rhinopteraspis* were imported into Blender for retrodeformation (Fig. 5). Use of Blender tools for retrodeformation followed the recommendations and techniques set out by Herbst et al. (2022). Initial retrodeformation focused on the best preserved plates and those with clearly delineated articulations (Lautenschlager et al., 2016), those being the rostral, orbital, supraoral and paraoral plates (Figs. 1-3). After rearticulating and repairing deformation, these elements provided a framework to delimit the dorsal and lateral extent of the oral plate array. The oral plates were aligned, maintaining their preserved order, within this delimited area by placing their dorsal

tips close to the margin of the mouth and rotating the plates posteroventrally to match the angle of the surrounding plates. The postoral plates were then fitted to the proximal ends of the oral plates. The proximal ends of the oral plates were then readjusted into articulation with the sulcus preserved in the postoral plates (Fig. 3C), while maintaining alignment with the closely articulated lateral oral- and paraoral plates and each other.Finally the ventral disc was retrodeformed and articulated with the postoral plate.

The reconstructed specimen was animated in Blender to simulate the movement of the oral plates Fig. 6). Empties (single geometry-less points that act as handles for object transformation without interfering in the render process) were placed between each oral plate and the postoral plate below, so that the local x-axis of each was aligned with the approximate outer boundary of the postoral plate. Each oral plate was then parented (=linked) to the empty below it. These empties were then animated to rotate around their local x-axes, causing the parented oral plate to also rotate around that axis.

3. Description

NHMUK PV P 73217 comprises an almost-complete three-dimensional specimen of *Rhinopteraspis dunensis*, preserving the entire headshield and articulated body scales (Fig. 1). The specimen has been crushed laterally during diagenesis, with the oral region and ventral shield having been pushed forwards and upwards (Fig. 1). Otherwise, the specimen is complete and individual oral elements appear to have maintained their original shape and relative location. The dermal plate anatomy of pteraspid heterostracans is well-characterised in numerous taxa (e.g. Blieck, 1984) and that of *Rhinopteraspis dunensis* NHMUK PV P 73217 broadly conforms with previous descriptions. The headshield is composed of large dorsal and ventral shields separated by paired cornual and branchial plates, with a dorsal spine set into the posterior margin of the dorsal shield (Fig. 1A-F). Anterior to the dorsal shield is an elongate rostrum that is separated from the dorsal shield by paired orbital plates (Fig. 1). The anterior length of the rostrum is broken off from the rest of the specimen (Fig. A,E,F). The unpaired pineal plate is indistinguishable from the top of the orbital plates in the scan data.

We adopt an anatomical terminology to clearly describe the oral apparatus of the specimen (Fig. 1G). For the anatomical axes of the animal as a whole we use dorsal/ventral in the dorsoventral axis, rostral/caudal for the sagittal axis, and dextral/sinistral for the transverse axis. When describing the oral apparatus itself we also use lateral/medial to describe lateral positions relative to to the sagittal axis, ad/aboral to describe the surfaces of plates relative to the direction of the oral opening/anus, and distal/proximal to refer to positions on the oral plates relative to their junction with the postoral plate.

The oral region is bordered dorsally by the supraoral plate, laterally by paired paraoral plates, and postero-caudally by the postoral plate (Figs 1D, 2). In previous descriptions of pteraspids, including *Rhinopteraspis*, the subrostral lamella and ascending postrostral lamella have been characterised as part of the rostral plate (Blieck, 1980; Tarlo, 1961). In NHMUK PV P 73217 they comprise a separate structure, broken into three parts (postmortem), which we term the supraoral plate (Figs 2A, 3A,B). The supraoral plate is trapezoidal in shape, narrowing rostrally. A pronounced furrow runs around its lateral and rostral margins, which was overlapped by the paraoral, orbital, and rostral plates; the

margins of the plate sweep ventro-caudally to form two latero-ventral arms (Fig. 3B). The anterior half of the ventral surface of the supraoral plate (the subrostral lamella) is smooth and slightly convex surmounted by a superficial layer of ornament (Fig. 1D). The caudalmost half (the ascending postrostral lamella) curves upwards into the mouth and lacks dentine ornament (as in *Rhinopteraspis cornubica* Tarlo, 1961, p. 373), the rostral border of this area presumably represents the position of the oral opening. This border is marked by a row of tubercles, comprising one large medial tubercle and two pairs of smaller tubercles on either side (Figs 1D, 3B). The paired paraoral plates are elongate and taper rostrally, and overlie large rostro-lateral overlap surfaces on the orbital plates, anterior to the orbits (Figs 2B,C, 3A). We reinterpret the 'olfactory grooves' identified in *Rhinopteraspis cornubica* by Tarlo (1961, fig. 1) as the overlap surfaces between the paraoral plates and supraoral plate (Fig. 3A).

The postoral plate is bow-shaped and originally symmetrical, although the right process is damaged (Fig. 3A,C). The ventral surface is smoothly convex. The dorsal surface has a posterior overlap surface that is concave to curve around the anterior rim of the ventral shield, and a dorsal surface which forms the ventral margin of the oral opening and bears paired sulci for the oral plates which are interrupted medially by a raised area (Fig. 3C). Paired lateral plates and lateral postoral plates lie between the postoral plate and the orbital plates (Figs. 2,3). The extensive overlap between the plates surrounding the mouth and the larger head shield plates strongly suggests that they comprised an integrated structural unit with little or no movement relative to each other.

The oral apparatus itself is composed of thirteen imbricated oral plates and one pair of lateral oral plates (Figs 2-4). These are arranged bilaterally about the midline into sinistral and dextral series. Although plate pairs that occur in equivalent positions on either side of the midline are similar, they do not exhibit mirror-image symmetry. In particular, the unpaired medial plate is not symmetrical but, rather, is continuous with the sinistral series (Fig. 3E,4). Each oral plate has the same general morphology of a main limb with a rhomboidal cross-section, a distal hook (except for the most laterally placed plates), and a proximal articulation surface for the postoral plate (Figs 3,4). There are seven oral plates in the sinistral series (termed L0-6) and six in the dextral series (termed R1-6), each preserved inclined at varying degrees (maximum about 45 deg) to each other along their coronal axis. The more medially placed the plate, the more inclined it is along its long axis to provide a fit with the adjacent oral plate; the lateral and medial faces of the plates overlap in an imbricated arrangement, inclined at decreasing relative angles for the plates in progressively more lateral positions. The hooks at the distal ends of the oral plates curve adorally, while the proximal ends of the plates are notched, reflecting the ventral limit of the ornament, serving as articulation with the postoral plate (except for the medial plate L0).

Figure 1. *Rhinopteraspis dunensis* NHMUK PV P 73217. A-D, photographs of complete specimen in (A) left lateral view with full length of preserved rostrum, (B) right lateral view, (C) close-up of front of head in left lateral view, and (D) close-up of oral region in ventral view; E-G, rendering of head shield based on computed tomographic data in (E) left lateral, (F) right lateral view, and (G) transparent with scheme of anatomical axes. Green and blue parts of 3D renders represent oral region. Abbreviations: L, left (sinistral), R. right (dextral). Scale bars represent 5 cm in panels A,B,E,F, 2.5 cm in panel C, 1 cm in panel D.

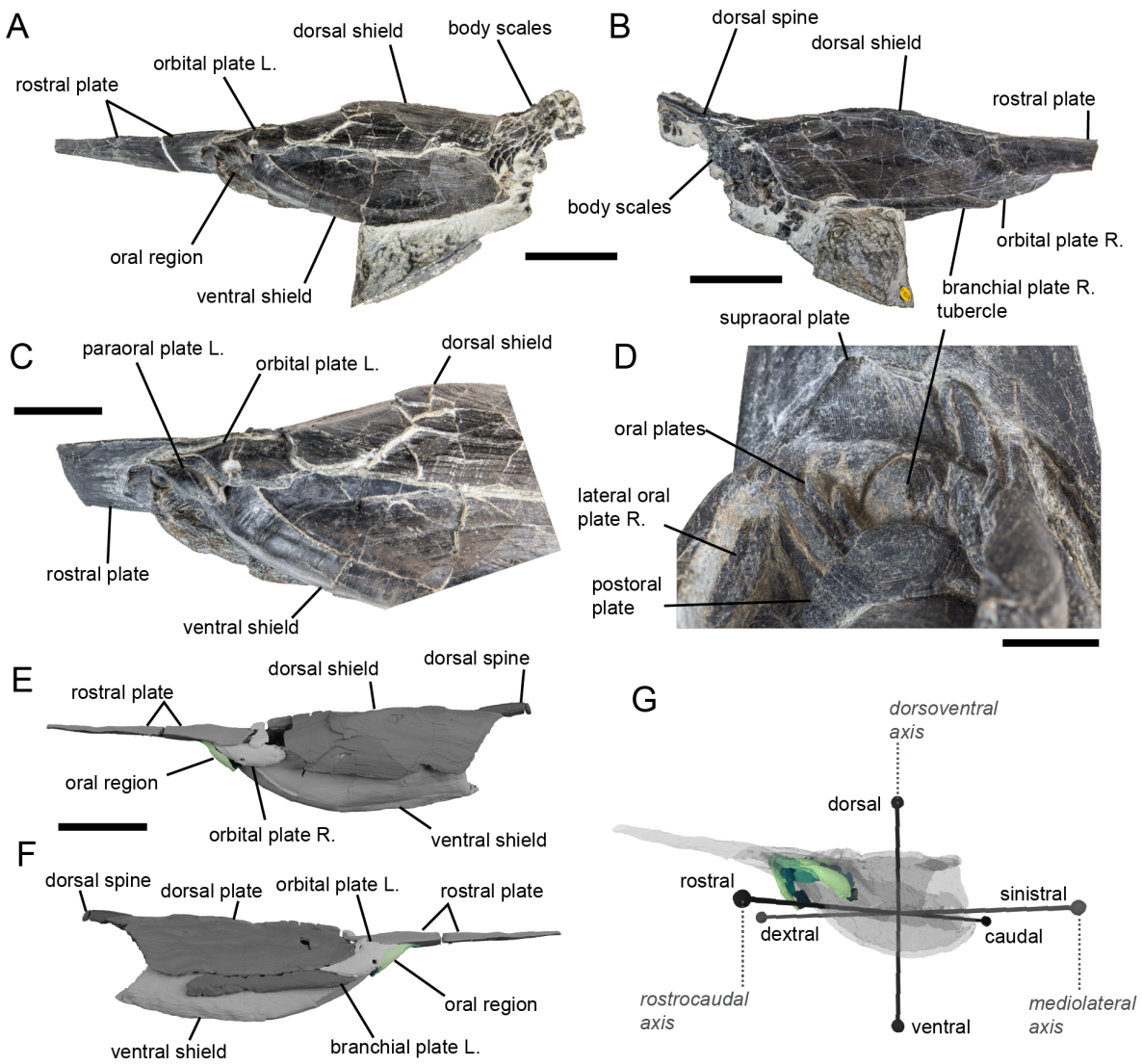


Figure 2. The oral region and surrounding area in *Rhinopteraspis dunensis* NHMUK PV P 73217 based on 3D renderings of computed tomographic data. A, ventral view; B, sinistral view; C, dextral view; D rostral view; E, Rostro-ventral view. Abbreviations: L, left (sinistral), R. right (dextral). Scale bars represent 1 cm.

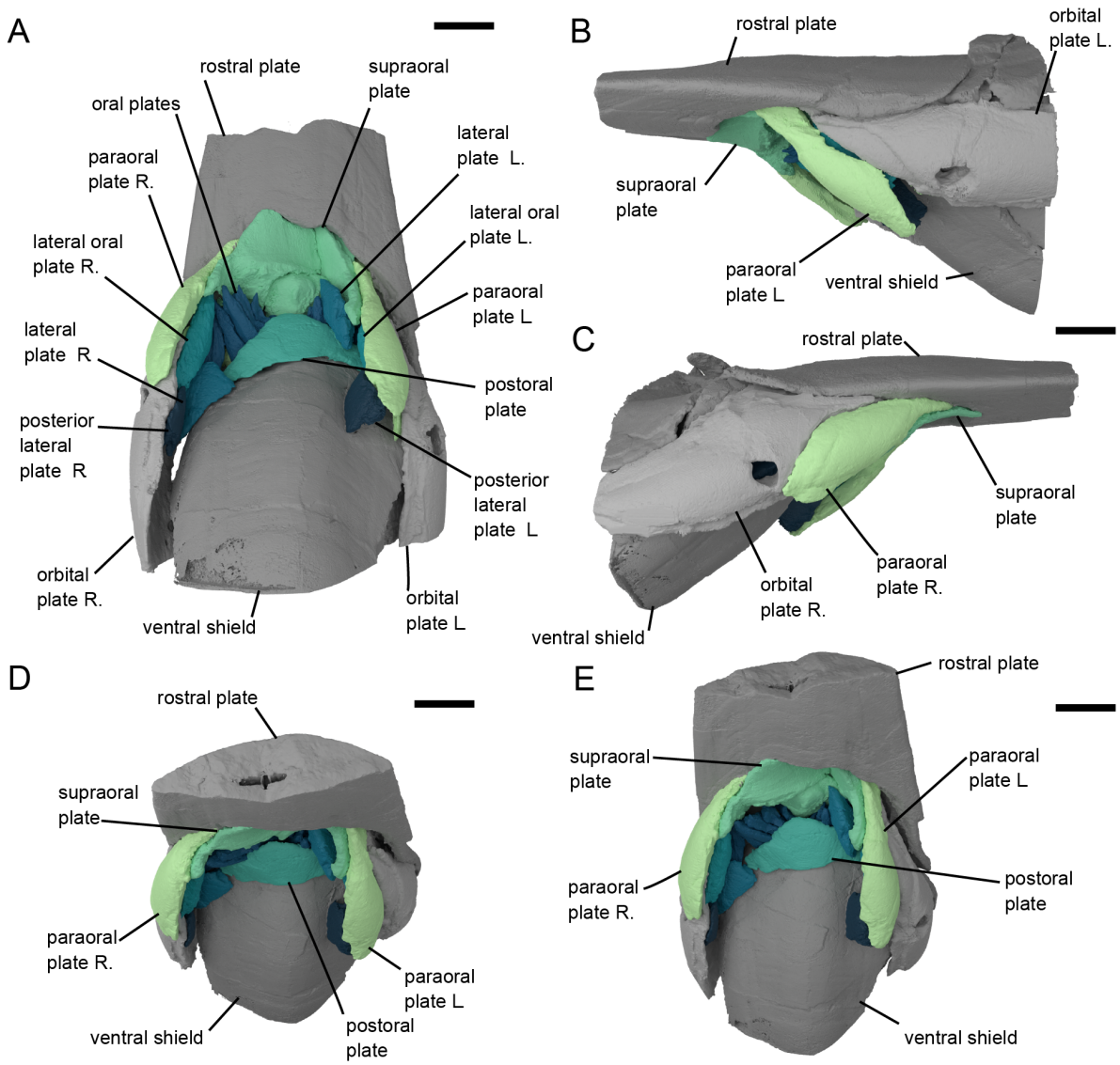


Figure 3. *Rhinopteraspis dunensis* NHMUK PV P 73217 oral region. A, oral apparatus and surrounding plates as preserved, in ventral view; B, ventral view of supraoral plate with three fragments rearticulated; C, postoral plate in dorsal view; D, oral apparatus as preserved with ventral plates removed; E, dorsal view of oral plates as preserved; F-I, oral plate R4 in adoral (F), lateral (G), aboral (H), and medial (I) views, alongside drawings depicting the inferred extent of dermal ornament in grey, based on comparison with isolated plates of *Loricopteraspis dairydinglensis*. Abbreviations: L, left (sinistral), R. right (dextral). Scale bars represent 1 cm in panels A-E, 0.5 cm in panels F-I.

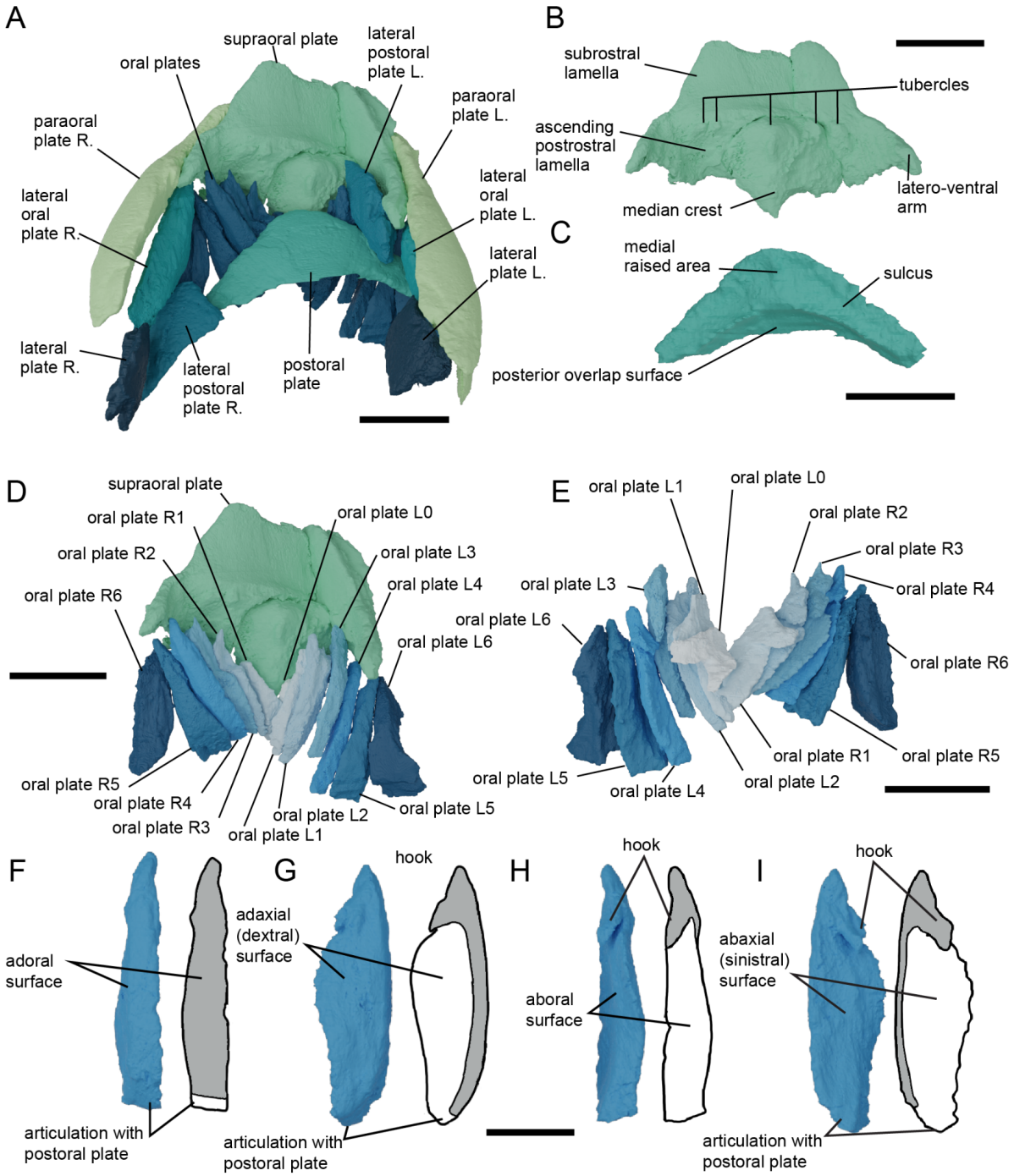
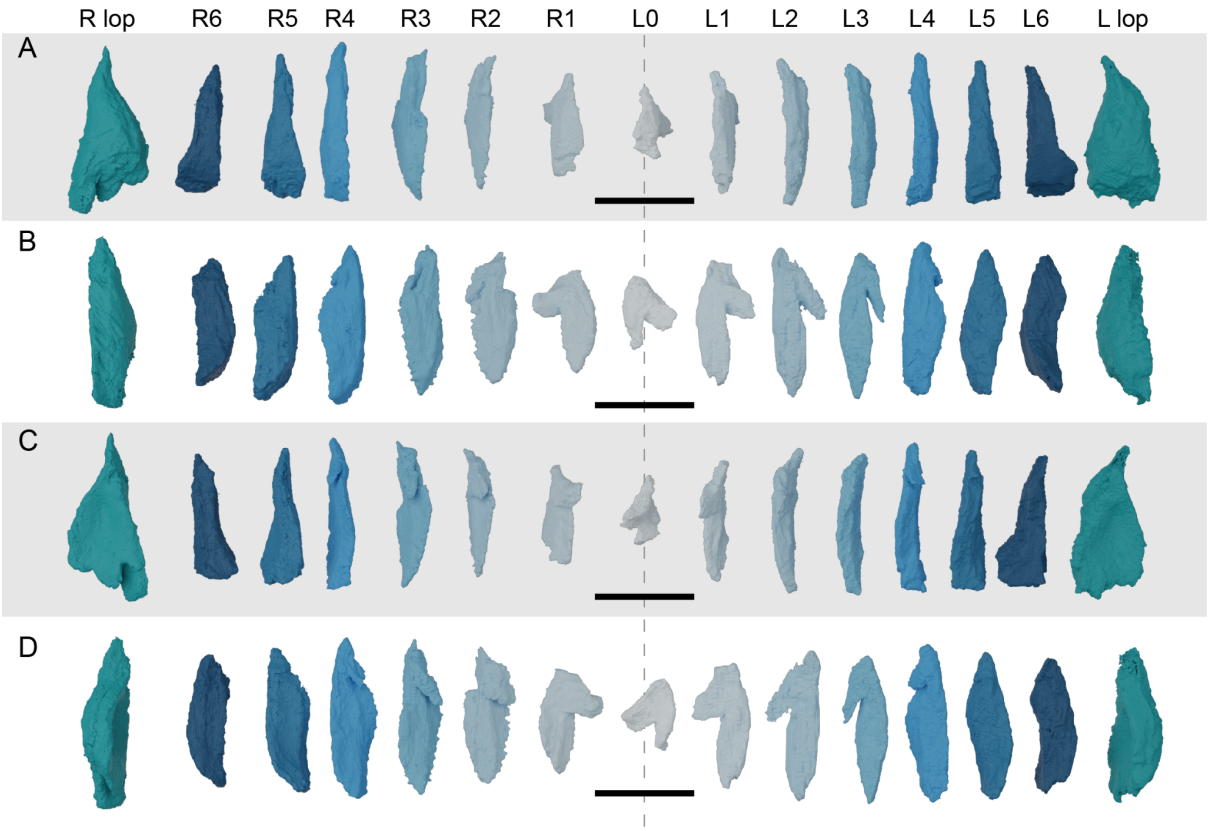


Figure 4 *Rhinopteraspis dunensis* NHMUK PV P 73217 oral and lateral oral plates in adoral (a), lateral (b), aboral (c), and medial (d) views. Dotted line intersects unpaired oral plate L0. Abbreviations: lop, lateral oral plate, L, left (sinistral), R. right (dextral). Scale bar represents 1 cm.



Although the oral plates have similar overall shapes, individually they vary in relative proportion depending on their position within the apparatus (Figs 3,4). The hook of the unpaired medial oral plate L0 is as long as the main limb. This plate is preserved overlying the lateral two oral plates R1 and L1. The lateral side of its proximal end is notched to fit with the left medial face of R1. Plate L0 curves to the right so it fits the curvature of the dextral face of the adjacent oral plate L1. The main limb of oral plates R1 and L1 are twice as long as that of L0 with a narrow base, and similarly may not have articulated with the pastoral plate, but the hooks are as large and very similar in shape. These plates fit around oral plates L2 and R2, themselves fitting around L3 and R3, these pairs have narrow bases and slightly smaller hooks than L1 and R1. Plates L4 and R4 have a slightly broader base and proportionally shorter hook than these plates. This trend continues laterally, with very short hooks and a very wide base in L5 and R5. Finally L6 and R6 have no perceptible hook and a very broad base. The lateral edge of Plates L6 and R6 is concave, fitting the medial edge of the lateral oral plates.

The lateral oral plates are morphologically distinct from the oral plates (Fig. 4), being roughly triangular, tapering rostrally with a curved medial margin that matches the lateral profile of the lateralmost oral plates (Fig.3A,4). The better preserved left lateral oral plate appears to have a distinct notch in its posterior side (Fig. 4A,C), although this is difficult to corroborate from the right lateral oral plate.

4. Reconstruction

The combined width of the bases of the oral plates, when aligned perpendicular to a sagittal plane, matches the length of the sulcus on the postoral plate (Fig. 5) and the complementary symmetry exhibited by adjacent plates indicates that they were capable of almost completely filling the width of the oral opening. In this position, the lateral-facing surface of each oral plate overlaps the lingual-facing surface of its outer neighbour (Fig. 5). The lateral surfaces of the outermost oral plates closely fit with the lateral oral plates (Figs. 5C,D). The most medial pair of oral plates appear to lie on top of the neighbouring oral plates rather than contacting the postoral plate. When viewed posteriorly, this brings the hooks of the plates into alignment, forming a plane above the posterior unornamented surface of the plates (Fig. 5d). This reconstruction also suggests that the oral apparatus fits together such that the tops of the oral plates extend to the top of the mouth to almost meet the supraoral plate. The medial crest of the supraoral plate creates a convex dorsal margin of the mouth, and the increasing length of the oral plates in lateral positions means that their dorsal tips also follow this convex line. Consequently the mouth would have been mostly covered by the oral plates, although the gaps between their tips would have left the mouth open to outside water (Janvier 1981). However there is no evidence that the plates intercalated with the tubercles demarcating the dorsal margin of the mouth at the rostral margin of the ascending postrostral lamella, Fig. 3B). When modelled to open around the axis of the sulcus on the postoral plate, the oral plates do not overlap as they rotate (Fig. 6). Instead, their placement along the curved axis of the postoral plate sulcus causes them to splay outwards (Fig. 6).

Figure 5. Reconstruction of *Rhinopteraspis dunensis based on* NHMUK PV P 73217, anterior section of rostrum not shown. A, anterolateral view; B, ventral view; C, anterior view; D, posterior view of articulated oral plates; E, sagittal cross-section through centre of head; F, close up cross-section lateral to E, showing junction between base of oral plate and the postoral plate.

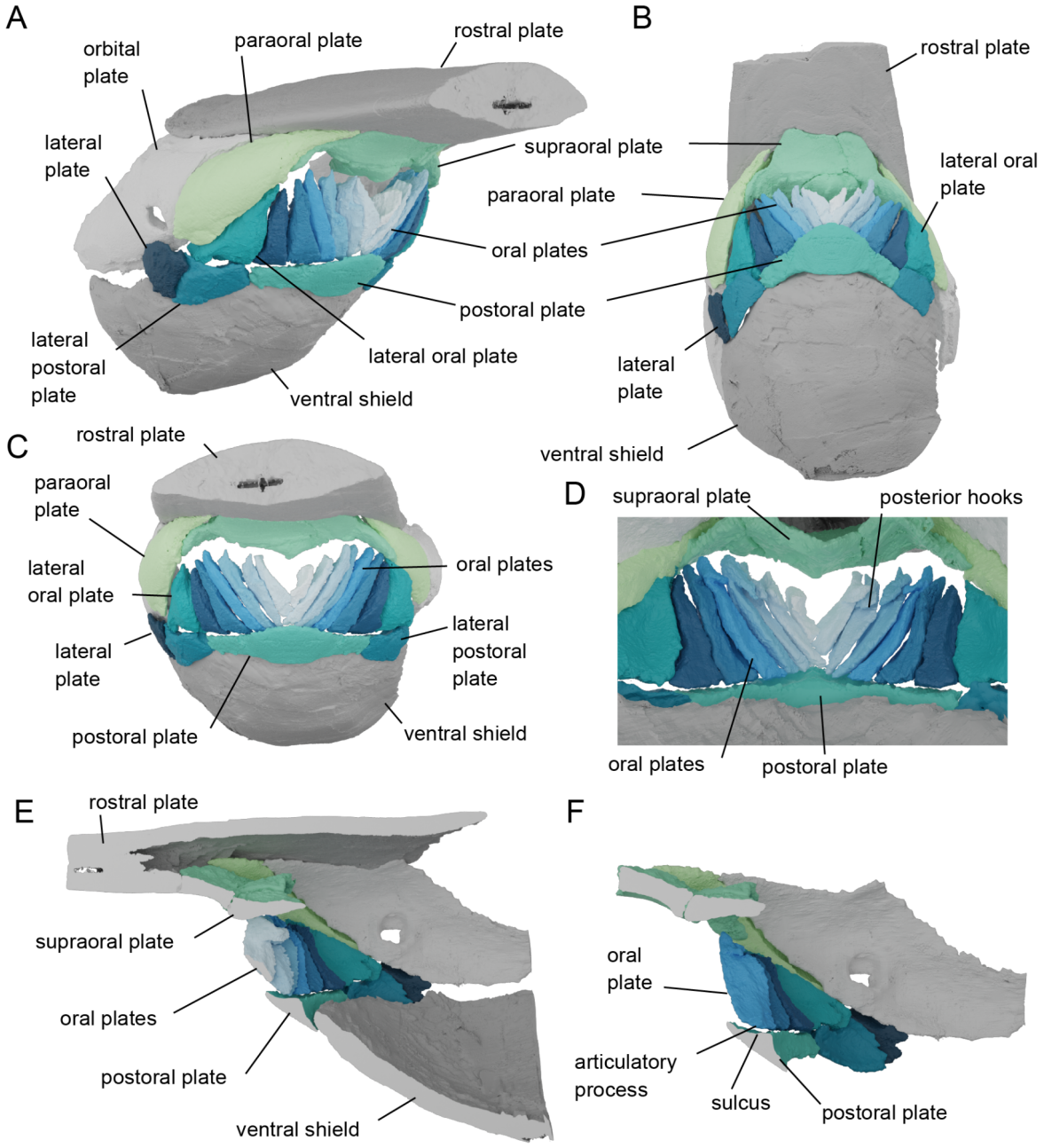
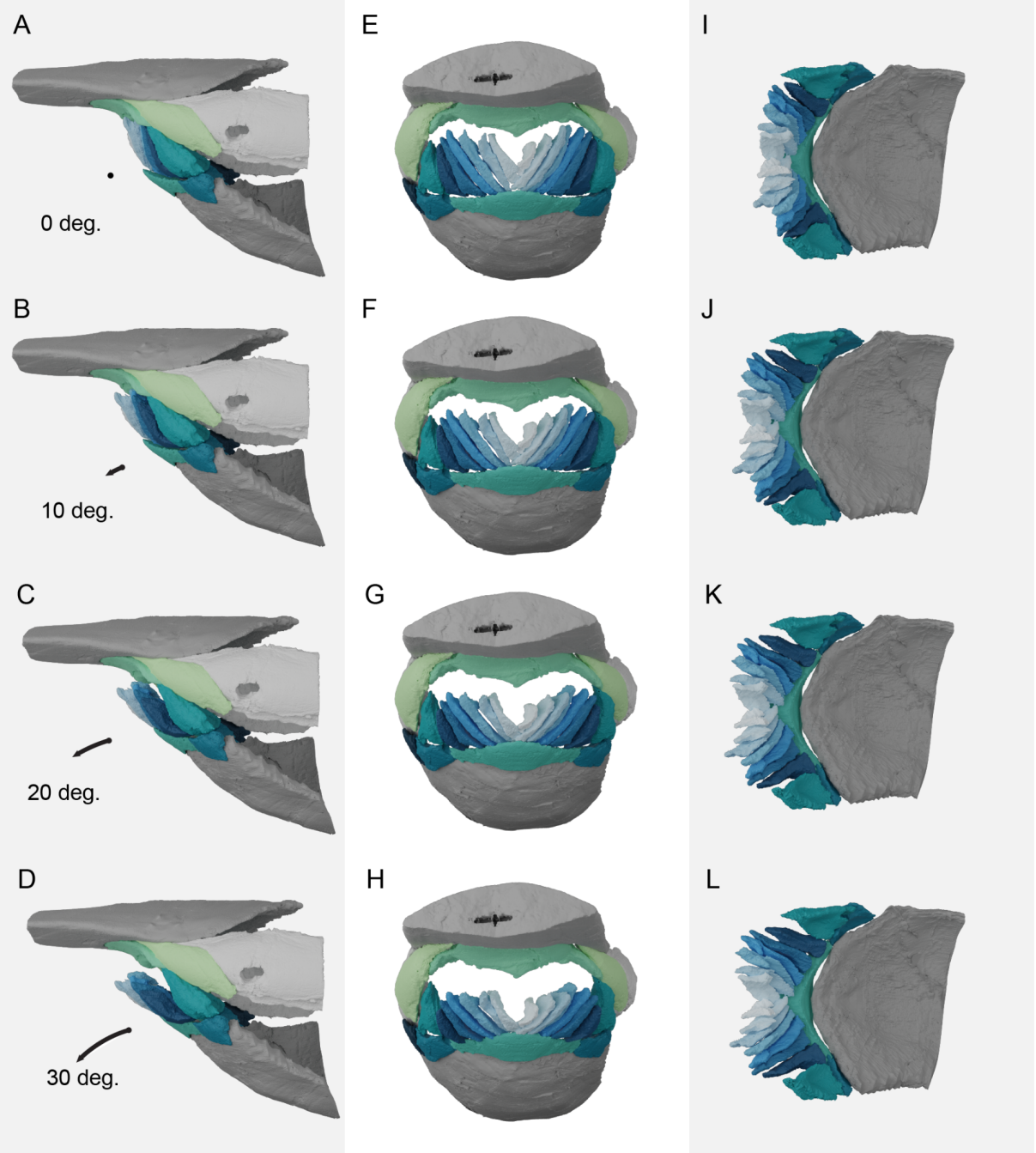


Figure 6. Reconstruction of *Rhinopteraspis dunensis* based on NHMUK PV P 73217 with oral plates animated to open to 30 degrees. A-D, lateral view; E-H , anterior view; I-L, dorsal view (with surrounding plates removed). A,E,I, resting position; B,F,J, open to 10 degrees; C,G,K, open to 20 degrees; D,H,L, open to 30 degrees.



5. Discussion

Based upon our 3D reconstruction of the oral region in *Rhinopteraspis*, we are able to consider the oral plates as an integrated apparatus and test hypotheses of its form and function. The endoskeleton of heterostracans is completely unknown beyond what can be inferred from the dermal skeleton (Janvier, 1993). In this interpretation we attempt to consider the constraints imposed by the dermal skeleton, without speculating as to the endoskeletal structure.

(i) Interpretation of the oral apparatus of *Rhinopteraspis*

Most previous hypotheses of function in heterostracan feeding assume significant movement and a degree of rotation of the oral apparatus, often following a cyclostome-like mode (Janvier, 1974, p. 197; Kiaer, 1928; White, 1935). In many of these the postoral plate(s) is assumed to move significantly, either inwards (Janvier 1974) or outwards (Janvier 1981, White 1935). The large, curved overlap surface at a 45° angle between the postoral plate and the ventral plate in *Rhinopteraspis* (Fig. 3C) suggests that this movement would not have been possible and that the postoral plate was static during feeding.

In contrast, the imbricated nature of the oral plates strongly suggests that they were mobile relative to the postoral plate. Any movement would have been a rotation around the point of their attachment to the postoral plate. The rhomboid cross-section and the complementary symmetry of the oral plates would have prevented them either moving independently, or moving in an entirely sagittal plane (Fig. 6). Rather, they must have moved as an integrated unit, splaying ventro-laterally as the plates rotated aborally on the sulcus of the postoral plate. The medial plates (L0) that do not articulate with the postoral plate are an exception: their cross-sectional shape and ab/adoral overlap would have precluded their movement relative to the other plates.

The morphologies of individual oral plates are closely comparable to those observed in acid-prepared isolated oral plates of *Loricopteraspis dairydinglensis* (Purnell, 2002; White, 1961). Comparison with these shows the distribution of ornament on the oral plates: of the four sides of the oral plate the anterior surface is covered in tuberculated ornament, as is the anterior part of the medial lateral surface and the sides of the hook (Fig. 3F-I). However, the lateral surfaces and the posterior surface of the oral plate, as well as the ventral side of the hook and the proximal end of the plate are unornamented, instead comprising a porous surface texture identical to that covering the visceral surface of body scales of pteraspidomorphs such as *Oniscolepis* (Märss and Karatajūtė-Talimaa, 2009). This indicates that these parts of the plates were embedded in soft tissue; the upper limit of this would have been the proximal surface of the large projecting hooks on the aboral side of the oral plates. The medial plates would have been supported entirely by this soft tissue. This soft tissue must have provided the basis of any movement of the plates and so may have comprised muscles or tendons.

At rest, this would have resulted in a narrow “letterbox-shaped” mouth, with the dorsal tips of the oral plates projecting into the gape. This morphology rules out a large gap for a hagfish-like prenasal sinus (Stensiö, 1964, 1958). There is also no evidence for separate upper oral plates as inferred by Stensio (1958, 1964). Based on such a reconstruction, the

forward facing denticles that Purnell (2002) identified on the adoral surfaces of the oral plates of *Loricopteraspis* would not have bordered the oral opening but rather the junction between the plate and its neighbour, linked by soft tissue. This ornamentation may have helped to prevent particles from becoming lodged in the spaces between the plates (Grohganz et al. in prep) and soft tissue and aided in cleaning the apparatus (Hamann and Blanke 2022). Any movement seems unlikely to have been great in magnitude due to the weak joint between the oral plates and the postoral plate, as well as the suspension of the small median oral plates in soft tissue. A structural analogue in a living vertebrate for heterostracan oral plates might be the branchiostegal plates in osteichthyans, which support the branchiostegal membrane, and make limited, coordinated movements to aid the suction pump (Farina et al., 2015).

The oral apparatus of *Rhinopteraspis* could only have been moved from the aboral side with rostro-caudal movements, as the adoral surfaces of the oral plates lack any kind of attachment surfaces. This is inconsistent with a gnathostome-like organisation of paired mandibular adductor muscles. However, living cyclostomes both operate the oral apparatus by moving cartilages rostrally and caudally along the floor of the pharynx. In hagfishes, keratinous toothlets are mounted on a cartilaginous dental plate that is pulled anteriorly along a basal plate to evert the lingual apparatus, and posteriorly to return it to resting position (Clark and Summers, 2007; Clubb et al., 2019; Dawson, 1963). In lampreys, a medial piston cartilage is protracted rostrally, moving a medial apical cartilage, the action of which brings keratinous toothlets in front of the apical cartilage into contact with other toothlets in a rasping action (Dawson, 1905a, 1905b; Hilliard et al., 1985). A medial groove along the visceral surface of the ventral shield in some pteraspids has been cited as evidence for a cyclostome-like medial structure of the oral mechanism (Janvier, 1993).

(ii) Implications for pteraspid feeding

Our articulated oral apparatus model can be used to consider the various feeding strategies that have been proposed for pteraspid heterostracans. These strategies can be roughly divided into macrophagy, predation, deposit/detritus feeding, and microphagy/suspension feeding (Purnell, 2001).

Hypotheses of macrophagous and predatory heterostracan feeding are based on analogy between heterostracan oral plates and the gnathostome mandible (e.g. Kiaer, 1928), or more rarely the hagfish oral apparatus (e.g. Janvier, 1974). However, the oral apparatus in *Rhinopteraspis* is poorly constructed for biting or grasping. Although the ascending lamella bears tubercles, which have been interpreted as the upper ‘jaw’ analogue in such a scenario (Tarlo, 1961), they do not occlude with the tips of the oral plates. Moreover, the angle of approach of the plates to the preoral plate during closing is oblique, with a low mechanical advantage, and would have been poorly suited to generating force. Finally, the oral plates themselves would not have formed a firm biting surface, with a poorly developed joint with the postoral plate even in the broad based lateral oral plates (e.g.plates L/R4-6) , and the medial oral plates (e.g. plates L0, L1, R1) suspended in soft tissue or with very narrow-based articulations with the postoral plate. Scenarios which see the oral plates as elements analogous to hagfish-like toothlets (Janvier, 1974) can be similarly ruled out by the junction between the proximal tips of the oral plates and the sulcus in the postoral plate, and the fixed position of the postoral plate.

Deposit/detritus feeding interprets the oral apparatus as a ‘scoop’ that would have been used to acquire sediment from the bottom of the water body (White, 1935). This requires the plates to evert substantially from their resting position, in White’s reconstruction including the movement of the postoral plate (White, 1935 figs 49, 50), or for the entire snout to be buried in the sediment. Based on our interpretation of *Rhinopteraspis*, this scenario can be ruled out based on the limited angle of opening of the plates and the constraining joint between the postoral and ventral plates. In *Rhinopteraspis* and in other long-snouted pteraspids such as *Errivaspis* this would also have been further hindered by the long snout (Fig. 1) and strongly convex ventral abdomen which would have restricted the ability of the animal to have placed its mouth in contact with the sediment. Snout length varies considerably in pteraspids and flatter, shorter snouted forms like *Loricopteraspis* (White 1961) may have been more readily able to interact with the substrate.

Instead, our reconstruction of *Rhinopteraspis* is only consistent with suspension feeding. This has convincingly been argued to be the most likely heterostracan feeding mode on the basis of wear patterns on the isolated oral plates of *Loricopteraspis dairydinglensis* (absence precluding deposit feeding) although Purnell (2002) did not speculate further on the nature of the suspension feeding organ itself. Notably, the outwards movement of the plates creates a greater area of gape than an anterior movement would, which would have increased water intake. In invertebrates such as rhynchonelliform brachiopods and some living oysters, zigzag deflections in the commissure between the valves prevents entry to larger particles while admitting smaller ones, and similar straining functions are present in animals as diverse as flamingos and gastropods (Rudwick, 1964). It is possible that the exposed tips of the oral plates in *Rhinopteraspis* acted as an analogous structure along with the tubercles on the supraoral plate. The limited movement acted to control the entry of larger particles into the mouth and may also have served to provide a means to expel larger particles trapped between the plates (Hamann & Blanke, 2022). Participation of the branchial arches in suspension feeding is currently unknown, as this region is only preserved in heterostracans as impressions on the internal dorsal shield surface.

(iii) Comparison of oral anatomy with other heterostracans

The anatomy of the oral apparatus of *Rhinopteraspis* is comparable to that of other pteraspids. Individually, the shape of the oral plates conforms closely to the morphologies of isolated plates acid prepared from an articulated specimen of *Loricopteraspis dairydinglensis* (White 1961, pl. 37; Groghanz et al. in prep). The arrangement of these plates is similar to articulated specimens of *Protopteraspis* (Kiaer 1928) and *Errivaspis* (White 1935). Importantly, the posterior alignment of the hooks in *Rhinopteraspis* (Fig. 3) can also be seen in other pteraspids where the adoral side of an articulated oral apparatus is visible: *Mylopteraspidella* (Stensiö, 1964, Fig. 44, p. 197) and *Protopteraspis* (Kiaer 1928), as well as in *Errivaspis* (White, 1935 figs 41-44). Together, these indicate that our interpretation of the feeding apparatus of *Rhinopteraspis* is more broadly applicable within pteraspids. However, varied body shapes and positions of the oral opening indicate some diversity in feeding ecology (e.g. *Doryaspis* (Pernegre, 2003), *Drepanaspis* (Gross, 1963)).

In non-pteraspid heterostracans the anatomy of the oral apparatus is far more varied. *Athenaegis*, the oldest articulated heterostracan often assumed to an outgroup to all other

macromeric heterostracans (Lundgren & Blom 2013, Randle & Sansom 2016, 2017, Elliott *et al.* 2021), has what are interpreted to be finger-like oral plates, and appears broadly anatomically consistent with *Rhinopteraspis* on the basis of our data (Soehn & Wilson 1990). By contrast, cyathaspids, a likely paraphyletic grade of heterostracans (Randle & Sansom 2017), have arrangements of plates which are difficult to homologise with those of pteraspids (e.g. *Anglaspis* (Blieck & Heintz 1983), *Poraspis* (Elliott & Petriello 2011), *Capitaspis* (Elliott 2013)). In amphiaspids, the oral aperture is instead a tube in a single, fused headshield (Novitskaya 1971). Meanwhile the oral apparatuses of the various "tessellate heterostracan" taxa are completely unknown (Dineley & Loeffler 1976). Many of these morphologies are difficult to reconcile with the pteraspid anatomy of *Rhinopteraspis* we describe here.Thus although it might be more widely applicable it is important to note that our interpretation of feeding is focused on *Rhinopterapis* and the closely allied long-snouted pteraspids. Further investigation is required to assess the ubiquity of suspension-feeding within the group, and the position in the water column at which they fed.

6. Concluding remarks

The absence of any information on the oral region in most Palaeozoic jawless vertebrate groups has placed pteraspid heterostracans at the centre of efforts to understand the feeding ecology in early vertebrates. Our three-dimensional reconstruction of the feeding apparatus of *Rhinopteraspis dunensis* suggests that movement of the apparatus was likely but limited to small movements of the finger-like oral plates. This is consistent with the idea of at least some heterostracans as suspension feeders, previously inferred on the basis of isolated oral plates, and suggests that the oral apparatus was more likely a means of moderating gape (Mallatt 1996). This finding is consistent with recent challenges to the prediction of New Head Hypothesis that vertebrate anatomy evolved in a predatory context (Ferron *et al.* 2022). However, the wide range of body shapes and oral anatomies present in heterostracans may indicate a variety of diets and ecologies. Study of other heterostracans may shed further light on the evolution of broader feeding mechanisms before jaws.

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Author contributions

SG, ER, ZJ, SL, and IS designed and conceived the project. Scans of *Errivaspis* were carried out by ZJ. RPD and SG carried out segmentation of the datasets. RPD and AJ carried out the retrodeformation of the specimen. RPD made all figures and wrote the initial draft of the manuscript, which all authors subsequently read and contributed to.

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