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A revised interpretation of the oral anatomy of *Athenaegis chattertoni* Soehn & Wilson (Vertebrata, Heterostraci) from the Silurian of Northwest Territories, Canada

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Abstract: Heterostracans are pivotal in examining the evolution of feeding and the head in jawed vertebrates as the stem-gnathostomes in which the oral apparatus is more commonly preserved. However, most analyses of their feeding, especially recent studies using modern 3D imaging methods, have focused on a specific subgroup, the Pteraspidiformes. *Athenaegis chattertoni* from the Wenlockian (Silurian) of Canada is the stratigraphically oldest heterostracan preserving an articulated feeding apparatus and is critical for reconstructing ancestral states in the lineage. Here, we use x-ray and synchrotron microtomography to re-examine the oral apparatus of *Athenaegis*, revealing a number of differences with the original reconstruction. Most importantly, the oral region of *Athenaegis* consists of numerous imbricated oral plates which functioned as a single integrated unit rather than a V-shaped arrangement separated by a medial seam. We show that *Athenaegis*, contrary to the original description, does not possess a medial postoral plate. The oral region was not capable of opening substantially as shown by the interdigitation of the oral plates, a close articulation with the surrounding plates, and an absence of muscle or ligament attachment points. We conclude a microphagous suspension feeding function of the oral apparatus for *Athenaegis* consistent with previous hypotheses of suspension feeding in heterostracans.

Key words: jawless fish, Palaeozoic, feeding mode, 3D reconstruction, Silurian, heterostracan.

JAWLESS vertebrates are a comparatively minor component of the present day vertebrate clade but dominated the fossil record during the early history of the group, with a wide range of armoured and unarmoured taxa from globally distributed Ordovician to Devonian strata (Janvier 1996). Heterostracans are the most abundant and well-documented of the armoured forms, which are collectively referred to as 'ostracoderms', and have assumed a textbook role in descriptions of early vertebrate evolution (e.g. Young 1962; Romer 1966; Benton 2024). Crucially, heterostracans are one of the very few ostracoderm groups in which the feeding apparatus is preserved in a number of taxa from across their phylogenetic and stratigraphic range (Purnell 2002). However, interpretations of these have largely been based on flattened, two-dimensional views of individual specimens with a particular focus on one taxonomic subset, the Pteraspidiformes. These investigations have elicited a broad spectrum of inferred feeding habits, ranging from predation (Kiaer 1928), to scavenging (Janvier 1974), to herbivory (Bendix-Almgreen 1986), to detritivory (White 1935) and to suspension feeding (see discussion in Purnell 2002), with a recent consensus emerging around the latter (Dearden *et al.* 2024, although see Grohganz *et al.* 2023, 2024). The role of feeding in determining the ecological rise of vertebrates, with an assumed progression towards predatory habits and increased activity as suggested in the New Head (Gans & Northcutt 1983; Northcutt & Gans 1983; Northcutt 2005) and New Mouth (Mallatt 1996) hypotheses, has been considered pivotal in the increasing dominance and size of the clade in ecosystems (e.g. Martik & Bronner 2021), although such propositions

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have been previously questioned by Purnell (2001, 2002). With this in mind it is important to document the breadth and variety of potential feeding styles of early vertebrates, which is reflected in part by their oral anatomy.

Athenaegis chattertoni Soehn & Wilson (1990), from the Wenlockian Delorme Group of the Mackenzie Mountains, Northwest Territories, Canada is the stratigraphically oldest heterostracan in which an articulated feeding apparatus is described. *Athenaegis* is interpreted as combining key character traits from the two major heterostracan groups, Cyathaspididae and Pteraspidiformes (Soehn & Wilson 1990). Because of this and its antiquity it has been important to forming phylogenetic hypotheses for the group (see e.g. Janvier 1996; Lundgren & Blom 2013; Randle & Sansom 2016, 2017; Elliott *et al.* 2021), and in doing so has often been assumed to represent an outgroup to macromeric heterostracans. The anatomy of the cranial skeleton and in particular the oral apparatus in *Athenaegis* is thus critical for reconstructing ancestral states in the heterostracans, in particular those pertaining to the oral apparatus. However, it has not been revisited since its original description.

Using high resolution computerized tomographic (CT and synchrotron) scanning, we re-examine a number of specimens of *Athenaegis*, including the holotype, to provide a revised description and 3D retrodeformed reconstruction of the head of the animal, with a particular emphasis on the structure and function of the oral feeding apparatus.

GEOLOGICAL SETTING

The type specimen and other articulated material of *Athenaegis chattertoni* were collected from the Avalanche Lake section AV1 in the Northwest Territories of Canada, with additional disarticulated material coming from section AV2. The fish come from Member 1R, a thin shale that is considered to represent a transgressive unit assigned to the Road River Formation (Soehn & Wilson 1990; Jin & Chatterton 1996). Member 1R is dated within the *patula/ranuliformis* conodont biozone (Over & Chatterton 1987), Sheinwoodian stage of the Wenlock (433.4–430.5 Ma). The shales and micrites of Member 1R are indicative of quiet water deposition and are underlain by Member 3W of the Whittaker Formation, which includes occasional bioclastic turbidites and is considered to represent basinal benthic assemblage (BA) zones BA 5–6 based on the invertebrate fauna (Over & Chatterton 1987). Member 1R is overlain by Member 1D, which is also assigned to the Road River Formation and represents shallowing conditions indicating a change from basin to slope to shelf (BA 3 or 4 in sections AV1–2) based on the invertebrate fauna (Over & Chatterton 1987).

MATERIAL & METHOD

Studied specimens

All material described here is housed in the collections of the Laboratory for Vertebrate Paleontology, University of Alberta (UALVP), Canada. The investigated specimens include UALVP 15682, UALVP 29926 and UALVP 33923. UALVP 15682 (holotype: Soehn & Wilson 1990, figs 4, 5C–E) constitutes a dorsoventrally flattened and almost complete specimen, with the ventral surface exposed and the rest of the specimen surrounded by matrix. UALVP 29926 (Soehn & Wilson 1990, fig. 5G; Fig. S1) is an isolated specimen largely free from matrix (other than infilling internal cavity) preserved three-dimensionally but laterally crushed and deformed. It comprises partial dorsal and ventral headshields, orbital plate(s), oral plates, partial branchial plates, and fragmented tail elements. UALVP 33923 (Fig. S2) has been largely transfer prepared out of the matrix and embedded in resin. The specimen consists of an almost complete head and part of the trunk but lacks termination of the tail. Similarly to UALVP 15682, it is extremely dorsoventrally compressed.

Computed tomography & visualization

UALVP 39923 and UALVP 29926 were scanned using a Nikon Metrology XTH 225ST x-ray CT machine at the XTM Facility, Palaeobiology Research Group, University of Bristol, UK. We scanned *Athenaegis chattertoni* UALVP 39923 twice, one scan targeting the anterior portion of the specimen (voltage: 115 kV, current: 94 μA, 3141 projections, 4 frames per projection, exposure: 1000 ms, no filtration, voxel resolution: 10.922 μm, stack dimensions: 515 X, 1910 Y, 1597 Z) and one scan targeting the posterior region (voltage: 95 kV, current: 147 μA, 3141 projections, 4 frames per projection, exposure: 1000 ms, no filtration, voxel resolution: 14.986 μm, stack dimensions: 794 X, 1851 Y, 2000 Z). We initially scanned specimen UALVP 29926 in Bristol targeting the oral region (voltage: 125 kV, current: 86 μA, 3141 projections, 2 frames per projection, exposure: 1000 ms, no filtration, voxel resolution: 10.668 μm, stack dimensions: 997 X, 1820 Y, 1831 Z). We additionally performed synchrotron x-ray micro-computed tomography on this specimen to further detail the three-dimensional oral plate morphology. Measurements of UALVP 29926 were taken on beamline BM18 at the European Synchrotron Radiation Facility (ESRF) in Grenoble, France (Schnetz *et al.* 2025). We used synchrotron radiation propagation phase contrast x-ray micro-computed tomography (SR-PPC-μCT), with an isotropic voxel size of 6.42 μm, and a sample to detector distance of 8 m (Weitkamp *et al.* 2011).

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The synchrotron current was 200 mA with a filtered white beam, with the beamline configured with 3.75 mm Molybdenum and 10 mm silicon-oxide block at 137 keV. For each 360 degree rotation, data acquisition was set to 8000 projections with a single exposure time of 30 ms. Data acquisition was carried out using an Iris15 camera (Teledyne Photometrics, Tucson, AZ, USA), and a 2000 µm-thick lutetium–aluminium–garnet scintillator. The final tomographic volume was reconstructed using PyHST2 (Mirone *et al.* 2014) and processed with the single-distance Paganin phase retrieval method (Paganin *et al.* 2002). The holotype, UALVP 15682, was scanned using a Nikon Metrology XTH 225ST x-ray machine at the Permafrost ArChive Science (PACS) CT laboratory at the University of Alberta, Edmonton, Canada. The whole specimen was scanned once (voltage: 220 kV, current: 60 µA, 3141 projections, 8 frames per projection, exposure: 125 ms, no filtration, voxel resolution: 20.066 µm, stack dimensions: 2000 X, 3163 Y, 956 Z).

The resulting image stacks were visualized in ImageJ v1.53o (Schneider *et al.* 2012) for cropping and improving contrast. Data were segmented in Avizo 2021.1 (ThermoFisher Scientific) and Mimics v23 (http://biomedical.materialise.com/mimics; materialize) to reconstruct the 3D morphology. Manual Avizo segmentation was completed via AI-assisted interpolation using the web-based application Biomedisa (Lösel *et al.* 2020). Avizo 3D models were visualized in MeshLab 2022.02 (Cignoni *et al.* 2008). Mimics surface meshes were exported into and imaged in Blender v3.4.1 (http://blender.org; Blender Foundation).

Retrodeformation

Segmented elements and fragments of *Athenaegis* specimen UALVP 29926 were imported as 3D models into Blender for retrodeformation (v3.0.0). Steps taken during retrodeformation followed processes described by Lautenschlager (2016) and Herbst *et al.* (2022). Although UALVP 29926 preserves 3D morphology, the overall morphology is distorted and disarticulated due to dorsoventral crushing and some mediolateral shearing in the oral region. The oral, orbital and rostral elements are disarticulated, fractured and incomplete, with extensive brittle deformation. The same applies to the dorsal and ventral shields; however these also suffer from plastic deformation. Techniques used to reconstruct the oral, orbital and rostral regions were limited to manual repositioning of elements, with no plastic alteration or rescaling of preserved material. In Blender, the 3D element meshes were rotated and translated to realign elements. Where CT segmentation had not separated individual elements or fragments sufficiently for accurate realignment, these were separated in Blender's Edit Mode using 'Circle Select' followed by the 'Mesh > Separate > Selection' sequence. Elements showing less severe disarticulation and those with obviously corresponding broken edges or articulatory surfaces were realigned first, as the best constrained basis for further rearticulation. In this initial stage the rostral, orbital and central dorsal shield elements were realigned. Next, the remaining dorsal, ventral and branchial regions were reconstructed; initially by realigning, then with Blender's sculpting tools ('elastic deform' and 'snake hook' specifically) to correct ductile/plastic deformation. Paired sinistral/dextral elements, in which one element was fragmentary or distorted, were replaced with a mirrored duplicate of the better preserved element. This reconstruction produced a well constrained oral region, into which the oral plates were realigned. Oral region reconstruction began with elements that retained approximate life articulation and position, followed by clusters of displaced but locally articulated elements, and finally individual disarticulated and displaced elements. Mediolateral order of oral plates was informed by their relative preserved positions and, for complete elements, their relative length. Identification of plates as sinistral/dextral was also based on preserved relative positions and on the direction of curvature along the longitudinal axis of the plate. Oral plate rearticulation was informed by preserved positions in the holotype (UALVP 15682; Soehn & Wilson 1990) and UALVP 33923. The rearticulated oral plates were inserted into the prior well-constrained retrodeformation; the oral plates and plates immediately surrounding the oral region were finally adjusted for best fit.

Some oral plates in UALVP 29926 are incomplete and obscure the exact plate articulations, therefore for testing hypotheses of oral opening a gestalt model was constructed combining the 3D morphology of oral plates in UALVP 29926 and the (complete, but flattened) articulations preserved in UALVP 33923. Oral plates from UALVP 29926, corresponding with those in UALVP 33923, were simplified, then adjusted to replicate the articulations preserved in the latter specimen. Where elements in UALVP 29926 were incomplete, an adjacent element was duplicated, scaled and adjusted to produce a complete oral region model.

Opening of the oral apparatus was simulated using the rotation manipulator tool in Blender. For this purpose, the centre of rotation was manually set to the articulating surface of each oral plate at its corresponding location along the ventral plate. Two configurations were tested with the oral plates: (1) moving as a single functional unit; and (2) hinging at the midline following Soehn & Wilson (1990) to test the feasibility of a V-shaped opening. Movement was simulated by manually rotating the respective units until a contact with another element was encountered or elements were forced to disarticulate. This

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was considered to represent the maximal opening achievable.

RESULTS

Using CT and synchrotron scans we are able to re-examine a number of features that have been previously described in *Athenaegis*. We largely follow the orientation terminology applied to *Rhinopteraspis* by Dearden *et al.* (2024) and Soehn & Wilson (1990) to the oral region. Our results are generally in agreement with the original description of Soehn & Wilson (1990), but differ significantly in terms of the overall organization of the apparatus. The material from Avalanche Lake is heavily compressed with most of the specimens of *Athenaegis* extremely dorsoventrally flattened (Fig. 1A, B). This has resulted in taphonomic damage and breakage as the various components of the dermoskeleton have interacted with each other under compression and are often fused post mortem. This is particularly evident in the holotype UALVP 15682, where the oral apparatus has been compressed against the internal curved dorsal headshield (Fig. 1C).

The oral region of *Athenaegis* is subterminal and anteroventrally located (Fig. 1A) and is delimited laterally by a pair of lateral oral plates (lop, Fig. 1G) and posteriorly by the ventral shield (vs, Fig. 1A–F). Anteriorly, a gap separates it from the rostral brim of the dorsal shield (ds, Fig. 1C–F). The oral apparatus itself consists of a series of paired oral plates (op) arranged in a V-shaped pattern across the sagittal axis of the apparatus. There is variation in the number of oral plate pairs between specimens (i.e. 7 pairs in UALVP 15682 and UALVP 33923, 8 pairs in UALVP 29926) without impacting on the gross morphology of the oral region. The majority of the individual oral plates are elongate, increasingly so laterally, with the smallest plate in UALVP 33923 (S. op1 in Fig. 1G) found at the leading (anterior, rostral) edge of the apparatus in the most medial position. The lateralmost oral plates (S. op6 & 7 and D. op6 & 7, Fig. 1G) are broader than op1–5 and exhibit multiple and occasionally oblique ornamental ridges. This may be the result of plate coalescence, although compression of the specimens obscures the detail in the CT scans needed to confirm this. The medial oral plates (op1–6) have a prominent ornamental ridge running up their long axis and the largest of these plates have a rounded, rostral, termination (most notable in D. op4–5 and S. op5–6); occasionally in UALVP 33923 these terminations are broken off and slightly displaced, resembling discrete elements (S. op5–6, Fig. 1G). The posteromedial edges of the largest oral plates imbricate with those on the other side of the apparatus. Posteriorly, the largest oral plates (D. op5–7 and S. op3–7, Fig. 1G) also meet the leading (anterior) edge of the ventral headshield (vs), while the smaller of the medial oral plates are only in contact with other oral plates (D. op4–1 and S. op2–1, Fig. 1G). The lateral oral plates (lop) are triangular in shape when viewed ventrally and possess multiple ornamental ridges (Fig. 1G). These are subsequently bordered by a pair of lozenge-shaped lateral plates (lp) followed by the arcuate suborbital 'epitegum' plates (sop) (Fig. 1E, F).

Although crushed and broken, the morphology of individual oral plates is best seen in UALVP 29926 (Fig. 2A). Three adjacent plates can be readily isolated, and they exhibit an ornamented aboral surface, which forms the broadest part of each individual plate. Their adoral, lateral and medial surfaces lack ornament and exhibit a porous surface texture, indicating that they were embedded in soft tissue (see Fig. 2K–S). In transverse cross-section, they taper from the ornamental surface towards their adoral termination, with a central cavity running up their midline (Fig. 2B, E). In both the 'as preserved' (Fig. 2B–D) and 'retrodeformed' positions (Fig. 2E–G) the individual plates are closely aligned. On their medial face, a series of vascular openings (red arrow, Fig. 2Q–S) confirm the position of the soft tissue contact here. Notably, there are no pronounced projections or hooks on the anterior margin or internal, adoral surface of these oral plates (Fig. 2F, N–P).

DISCUSSION

Interpretation of the oral apparatus

The oral apparatus of *Athenaegis* was originally reconstructed by Soehn & Wilson (1990) as comprising multiple paired oral plates arranged in a V-shape, separated by a straight medial seam, with a singular small postoral plate. Our CT-based reconstructions of UALVP 15682 and UALVP 33923 clearly demonstrate that individual oral plates are imbricated across the medial line of the apparatus (Figs 1B, C, G, 3A, C, S2, S4), which contrasts with the original reconstruction (Soehn & Wilson 1990, figs 4, 8). The medial seam inferred in the previous interpretation seems to be an artefact of missing material due to specimen damage (see Fig. S4). A medial seam is not present in other heterostracans with multiple oral plates, and *Athenaegis* seems to conform to what is considered a predominately pteraspid model (Kiaer 1928; Purnell 2002; Randle & Sansom 2017). Our reconstruction also shows that there is no postoral plate in *Athenaegis*. The structures referred to by Soehn & Wilson (1990) as 'post-oral' in the holotype UALVP 15682 and another, unspecified, specimen appear to be broken and displaced fragments of oral plates ('p-o', Fig. 1C, E).

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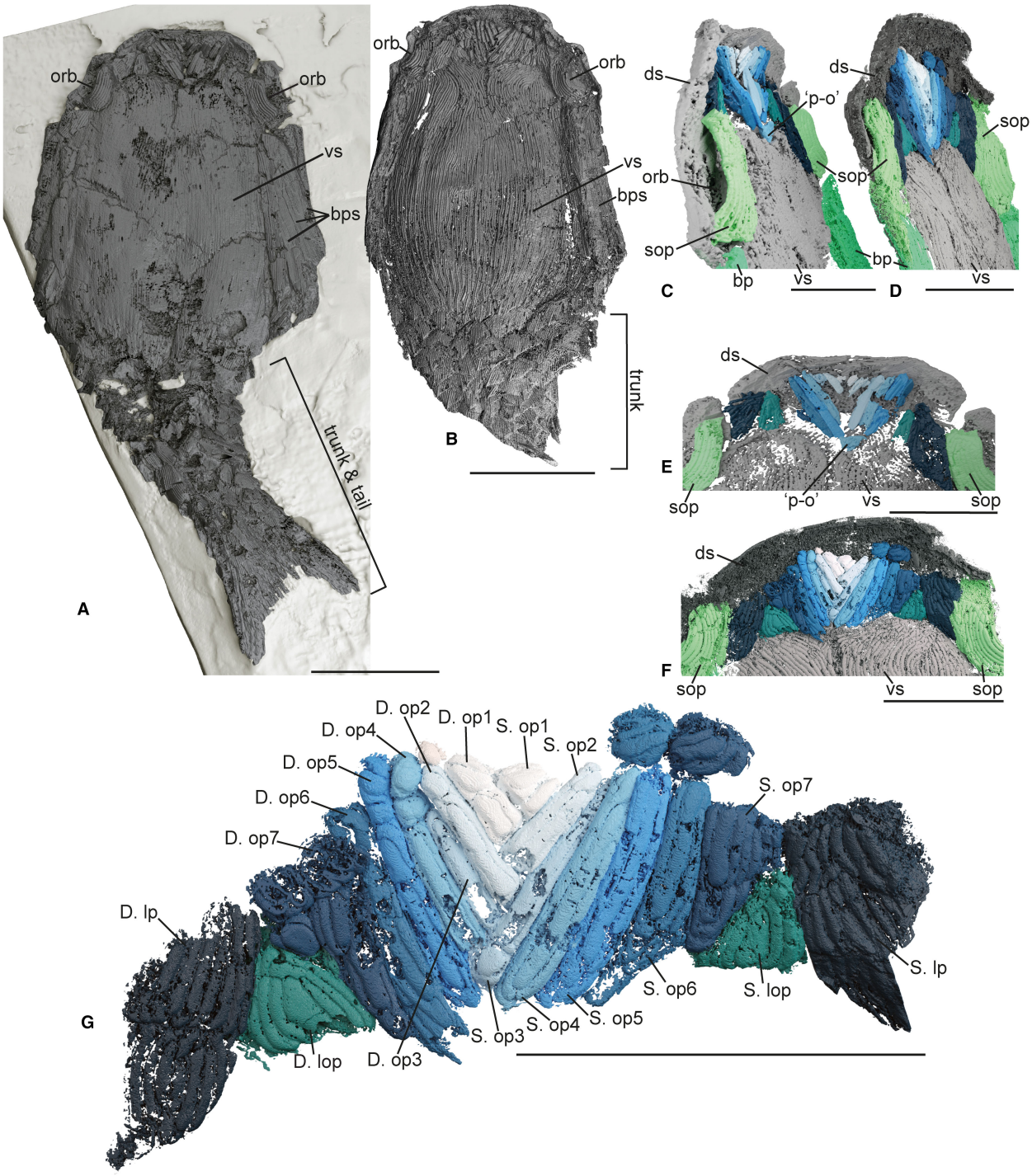


FIG. 1. *Athenaegis chattertoni* Soehn & Wilson 1990, Road River Formation, Wenlockian, Silurian. A, surface render of holotype UALVP 15682 in ventral view. B, surface render of UALVP 33923 in ventral view. C, lateral view of holotype UALVP 15682 illustrating crushing and damage to oral plates against the curved dorsal headshield. D, lateral view of UALVP 33923 (compare with C). E, oral region of holotype UALVP 15682 in ventral view. F, oral region of UALVP 33923 in ventral view. G, oral and lateral plates of UALVP 33923. *Abbreviations*: S, sinistral; D, dextral; bp, branchial plate; bps, branchial plates; ds, dorsal shield; lop, lateral oral plate; lp, lateral plate; op, oral plate; orb, orbit; 'p-o', described as a postoral plate by Soehn & Wilson (1990); sop, suborbital plate; vs, ventral shield. Scale bars represent: 1 cm (A, B); 2.5 mm (C, D); 5 mm (E–G).

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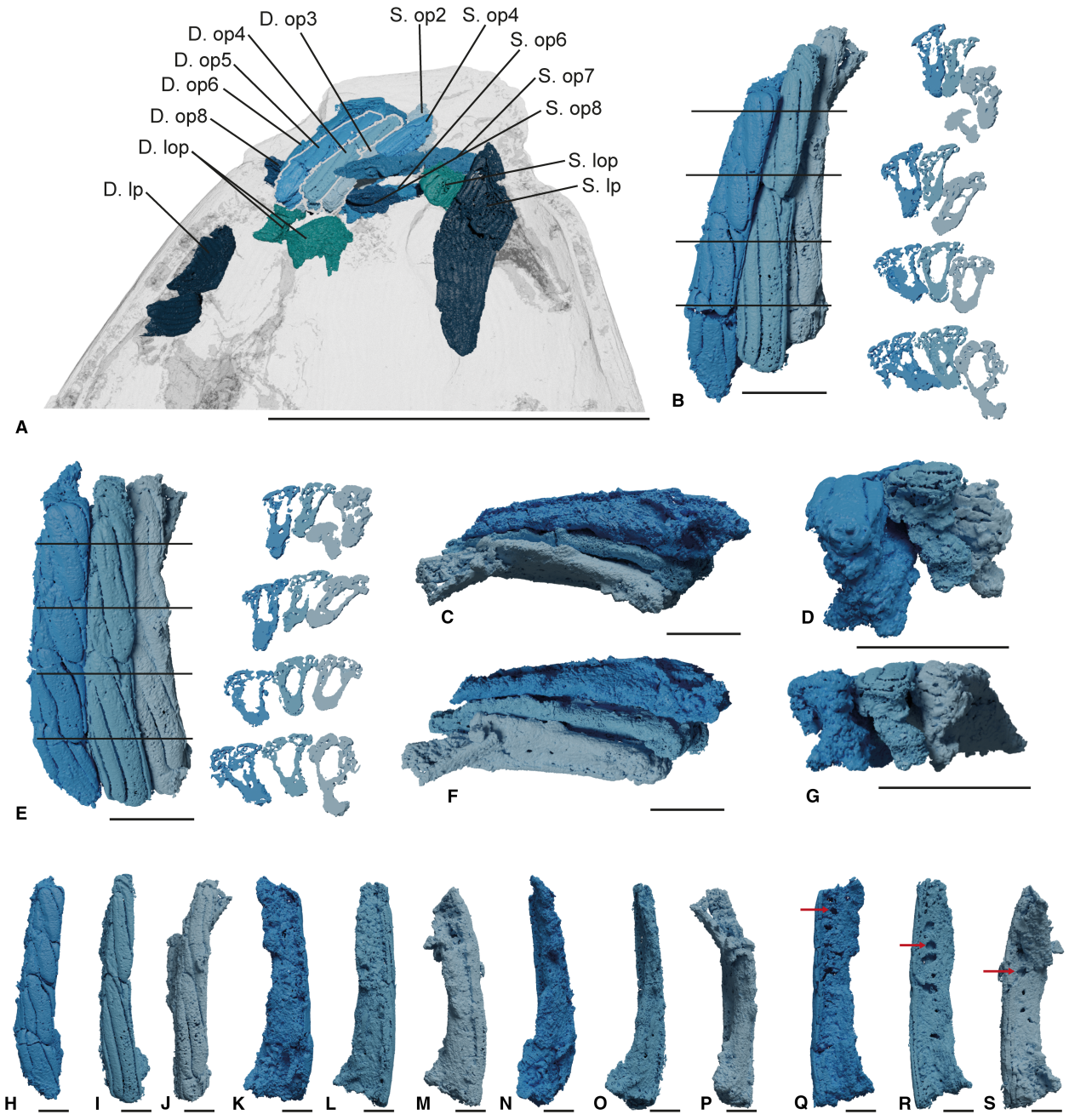


FIG. 2. *Athenaegis chattertoni* Soehn & Wilson 1990, Road River Formation, Wenlockian, Silurian (UALVP 29926). A, position of the oral elements (coloured) in the anterior of the specimen; those outlined in white comprise the rest of figure. B–D, oral elements as preserved in the specimen: B, aboral view with transverse virtual cross sections to the right; C, adoral view; D, posterior view. E–G, oral elements retrodeformed to illustrate assumed life position: E, aboral view with transverse virtual cross sections to the right; F, adoral view; G, posterior view. H–S, individual oral element morphology in: H–J, aboral; K–M, lateral; N–P, adoral; Q–S, medial view. Red arrows (Q–S) indicate vascular openings. *Abbreviations*: S, sinistral; D, dextral; lop, lateral oral plate; lp, lateral plate; op, oral plate. Scale bar represents 1 cm in (A), 1 mm in (B–G), and 0.5 mm in (H–S).

Soehn & Wilson (1990) interpreted the apparatus as forming a broad scoop-shaped opening, with individual plates articulating with their antimere along their proposed medial or midline seam, with the leading edge of the apparatus forming a V-shape in anterior view. As noted, our reconstruction does not support the presence of such a midline seam as the oral plates interdigitate with those of the opposite side (Figs 1G, 4B, S2; this

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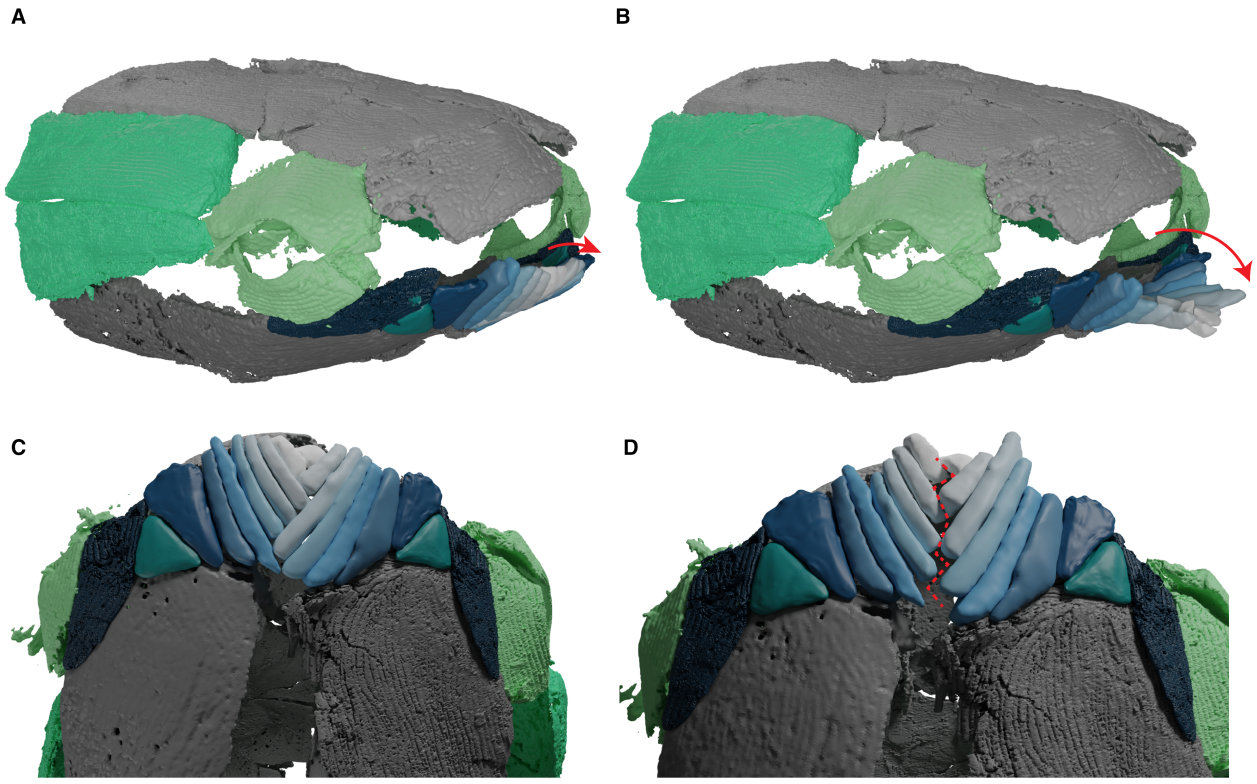


FIG. 3. Composite reconstruction of the oral opening of *Athenaegis chattertoni* based on UALVP 29926 (oral and lateral oral plates) and UALVP 33923 (lateral, orbital, suborbital, branchial, dorsal and ventral plates). A, C, oral opening based on this study. B, D, oral opening following Soehn & Wilson (1990). Arrows indicate extent of oral plate opening. Dashed line (D) shows the dislocation and 'un-zipping' of the individual oral plates to accommodate the Soehn & Wilson (1990) reconstruction. A–B, anterolateral views. C–D, ventral views.

arrangement is also seen in the holotype despite the oral region being incomplete, Fig. S4). Consequently, this rules out the dislocation and 'un-zipping' of individual oral plates required for the reconstruction in Soehn & Wilson (1990) (see Fig. 3B, D). Instead, anterolateral rotation of the individual plates would have been extremely limited or absent. The apparent coalescence of the lateralmost oral plates puts further restrictions on the opening of the oral apparatus (Fig. 1F, G). Similar oral plate fusion has been noted in pteraspids (i.e. *Protopteraspis*) by Purnell (2002; specimen illustrated in Purnell 2003, fig. 2). This lateral fusion of individual plates mitigates against the broad opening of the whole apparatus in a scoop-like function (Purnell 2002). Based on these observations, we interpret the oral apparatus as functioning as a single integrated unit, with the oral plates maintaining their position and orientation relative to each other. The oral apparatus had a limited range of dorsoventral movement relative to the ventral shield, with slight expansion relative to the oral lateral plates (Fig. 4; Video S1).

Our interpretation of these multiple oral plates as performing a single, integrated function, is corroborated by the anatomy of the oral region morphology of some other cyathaspids. In *Poraspis* (Elliott & Petriello 2011) and *Capitaspis* (Elliott 2013), a single large, broad oral plate lies anterior to the ventral shield, flanked by lateral oral plates.

Comparison of the oral apparatus to the pteraspid 'model'

Pteraspids have long served as the principal model for interpretations of heterostracan feeding (White 1961; Purnell 2002; Grohganz *et al.* 2024), although the pteraspid *Rhinopteraspis* is the only heterostracan in which the oral apparatus is known in detail and 3D (Dearden *et al.* 2024). As Soehn & Wilson (1990) recognized, the oral plates and apparatus of *Athenaegis* generally resemble those of pteraspids such as *Rhinopteraspis* (Dearden *et al.* 2024) and *Loricopteraspis* (White 1961; Purnell 2002). As in pteraspids, the oral plates do not open out along a medial seam (as reconstructed in Soehn & Wilson 1990). *Athenaegis* also does not exhibit a firm biting surface and the oral plates would have occluded poorly with the dorsal shield, another functional feature in common with pteraspids. In addition, the curved

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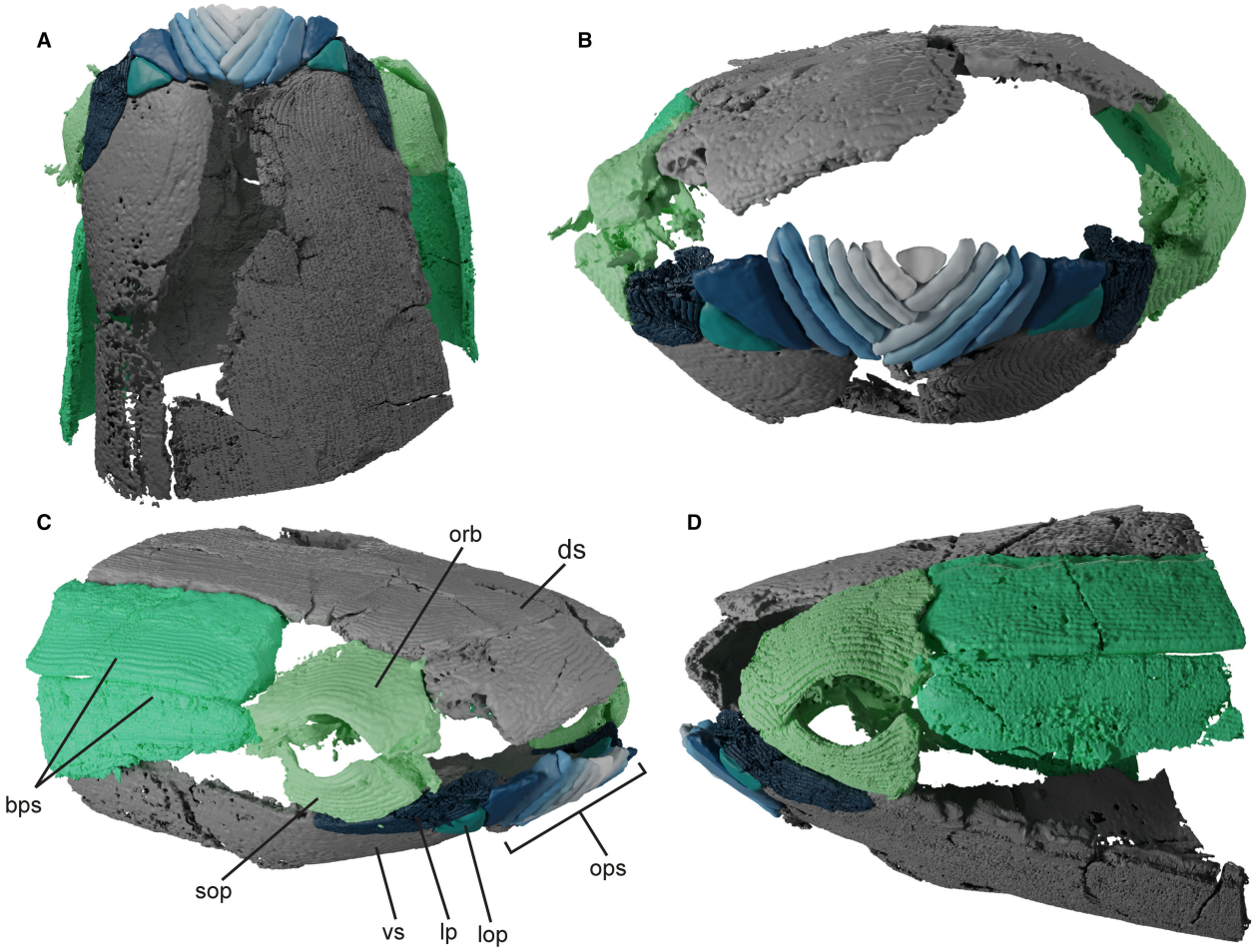


FIG. 4. Composite 3D reconstruction of *Athenaegis chattertoni* based on specimens UALVP 29926 (oral and lateral oral plates) and UALVP 33923 (lateral, orbital, suborbital, branchial, dorsal and ventral plates). A, ventral; B, anterior; C, anterolateral; D, sinistral view. *Abbreviations:* bps, branchial plates; ds, dorsal shield; lop, lateral oral plate; lp, lateral plate; ops, oral plates; orb, orbital plate; sop, suborbital plate; vs, ventral shield.

anterior margin of the dorsal shield, in conjunction with the straight anterior margin of the oral plate unit, suggests the presence of a permanent terminal gape at the oral opening. Our data show that *Athenaegis* lacks the prominent adoral distal hooks observed in pteraspid oral plates (White 1961; Grohganz *et al.* 2023; Dearden *et al.* 2024). These hooks have been linked to muscle attachment and mechanical performance of the oral plates (White 1935; Denison 1961; Tarrant 1991; Dearden *et al.* 2024; Grohganz *et al.* 2024). Furthermore, the broad postoral plate of *Rhinopteraspis*, which provides the articulation surface for the outward rotation of the oral plates (Dearden *et al.* 2024), is absent in *Athenaegis*. Additionally, *Athenaegis* lacks the elongated rostral region ('snout') prominent in some pteraspids which may aid in feeding. However, a relationship between head shapes and potential feeding modes in heterostracans has yet to be investigated. Thus, *Athenaegis* diverges further from the pteraspid model than has previously been recognized, although a number of common features can be identified, including the presence of a permanently open slit-like gape but with limited potential for expansion.

Implications for feeding ecology in Athenaegis

Previous hypotheses for heterostracan feeding ecologies have included predation, herbivorous macrophagy, detritus feeding and suspension feeding (see Purnell 2002 for a summary). Detailed analysis of articulated (Dearden *et al.* 2024) and isolated (Purnell 2002) pteraspid oral plates have considered suspension feeding as the most likely mode, although there is some suggestion that the oral plates are adapted to a mechanical function (Grohganz *et al.* 2024). Our revised interpretation of the oral morphology of *Athenaegis* presented here does not

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support a biting mechanism. As in *Rhinopteraspis*, the construction of the apparatus is poorly suited to biting and there is no clear evidence for the muscle attachment which is necessary to create any strong dorsal–ventral biting movement. This also applies to herbivorous feeding considerations, which are mainly based on comparison of overall body shape to that of extant osteichthyans, and require the oral plates to shear against each other to process algae (Bendix-Almgreen 1986). Our reconstruction of the oral apparatus of *Athenaegis* functioning largely as a single unit further refutes this hypothesis. We rule out macrophagy as a mode of feeding in agreement with the previous interpretation of Soehn & Wilson (1990).

However, contrary to Soehn & Wilson (1990), we consider it unlikely that *Athenaegis* was a detritivore. Detritus feeding has been proposed for heterostracans (e.g. White 1935; Janvier 1981) and specifically in *Athenaegis* (Soehn & Wilson 1990), and involves scooping up substrate from the sea floor, often with the mouth forming a type of shovel or scoop. This motion would have involved a significant protrusion of the oral plates, which can be rejected based on our data. Presence of ornamentation on all sides has been proposed to indicate free movement of individual oral plates (White 1935), allowing them to expand to form a scoop for feeding. However, the oral plates of *Athenaegis* do not have ornamentation on all sides, only on the aboral surface. Deposit feeding may also involve burial of the mouth into the substrate, which cannot be ruled out in *Athenaegis* solely on the basis of oral plate morphology. The presence or absence of wear on shield elements can give an indication as to whether repeated contact with the substrate has occurred (White 1935; Denison 1973), as shown in one *Poraspis* cf. *P. polaris* specimen (Dineley & Loeffler 1976), in *Allocryptaspis* (Elliott *et al.* 2004) and in *Loricopteraspis* (Grohganz *et al.* 2024). We note that Purnell (2002, p. 84) described (although did not illustrate) the presence of only a few indistinct scratches on the oral plates of *Athenaegis*, which he found problematic in their functioning as a scoop in a detritus feeding scenario. Similarly, we have not observed organized wear on the oral apparatus or ventral shield of any of the investigated specimens of *Athenaegis*, although this may be limited by the resolution of the scans. Recent finite element and microstructural analyses (Grohganz *et al.* 2024) have been used in support of a mechanical function for adoral hooks in pteraspids related to an interpretation of deposit feeding. Irrespective of this interpretation, there are no hooks present in *Athenaegis*. Furthermore, trace fossils could provide evidence of interactions with the substrate (Soehn & Wilson 1990). Despite the abundance of heterostracans in shallow water depositional environments, which are often rich in trace fossils, no clear ichnotaxa documenting any associated detritus feeding activities are currently known. Two putative ostracoderm trace fossils have been proposed, both from the Ordovician, although both occurrences fall outside of the known stratigraphic range of heterostracans. Fischer (1978) interpreted a trace named *Agnathichnus* from the Harding Sandstone as resulting from the feeding behaviour of the jawless fish *Astraspis*. However, we agree with Elliott *et al.* (1991) in questioning this interpretation given the morphology of the trace and what is currently known about the morphology of Harding Sandstone ostracoderms. A more recent description of a potential ostracoderm trace from the Cobb Formation (Tremadocian – early Darriwilian) of Western Australia (Haines *et al.* 2022, fig. 14) is likely to record the whole body resting on the substrate rather than actively feeding on or within the substrate. Currently, the lines of evidence presented here support the rejection of a detritus/deposit feeding style in *Athenaegis* (see also Purnell 2002).

Having ruled out all but suspension feeding (a conclusion also reached by Purnell 2002), this presents a conundrum. Extant mandibulate aquatic vertebrates rely to a greater or lesser extent on modification of their oral region and pharynx to achieve food acquisition via suction, ram and biting either alone or in concert (Ferry *et al.* 2015). Oral cavity expansion from the anterior to posterior in modern fish involves multiple parts of the skull (Kane *et al.* 2019), but *Athenaegis* and other heterostracans are constrained by their dermal armour and thus would not have such capacity. A lack of modern analogues means that, in order to avoid too much speculation, all we can say is that water with suspended particles of food can enter the mouth and be filtered/processed in some way by the gill arches, which are known to be extensive in heterostracans based on internal impressions on the dorsal and ventral headshields (see Janvier 1996).

The reconstruction of the oral apparatus of *Athenaegis* as presented here depicts a number of oral plates functioning as a single integrated unit with substantially limited outward movement, forming a dorsoventrally narrow but laterally extensive opening. Based on this and rejection of the feeding strategies outlined above, the oral morphology of *Athenaegis* is most congruent with microphagous suspension feeding, which is also consistent with more recent heterostracan feeding hypotheses (Purnell 2002; Dearden *et al.* 2024).

Broader implications for the range of feeding modes in heterostracans

The phylogenetic position of *Athenaegis* within heterostracans makes it particularly important for understanding the evolution of the oral apparatus in the group. Phylogenetic discussions of the Heterostraci that have included

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Athenaegis have variously considered them in the tolypelepids (a seemingly obsolete paraphyletic grouping as the sister group to the cyathaspids; Soehn & Wilson 1990; Janvier 1996), as a singular outgroup to the cyathaspids (Lundgren & Blom 2013; Elliott *et al.* 2021), as an outgroup to all higher heterostracans (Randle & Sansom 2016, 2017), and most recently within the cyathaspids (Randle *et al.* 2025). While the focus of the current paper is not systematic, there are a number of observations that can be made based on the oral apparatus (Fig. 5).

As mentioned above and discussed by Soehn & Wilson (1990), the gross anatomy of the oral apparatus of *Athenaegis* bears a number of striking similarities with those of pteraspids. These include the presence of multiple elongate oral plates, such as seen in *Pteraspis*, *Protopteraspis*, *Rhinopteraspis*, *Loricopteraspis* and *Errivaspis* (Kiaer 1928; White 1935; Purnell 2002; Dearden *et al.* 2024). Despite this superficial similarity, the oral plates of *Athenaegis* do not appear to be capable of the independent movement and fan-like projection as reconstructed for *Rhinopteraspis* (Dearden *et al.* 2024). The fan-like pteraspid oral apparatus is characterized by the addition of musculature and separation of individual oral plates both individually and along the midline, as well as the addition of an independent postoral plate posteriorly. Those cyathaspids that are characterized by one broad oral plate presumably result from fusion of multiple individual plates into a single unit. By functioning as a single unit, the oral region in *Athenaegis* more closely resembles cyathaspids such as *Poraspis* (Fig. 5; Elliott & Petriello 2011) and *Capitaspis* (Elliott 2013).

The condition in *Athenaegis* could be interpreted as the plesiomorphic state from which the oral apparatus of 'higher' heterostracans evolved, as suggested by a sister group relationship to the cyathaspids and pteraspids (Fig. 5A; Randle & Sansom 2017), although alternative phylogenetic treatments nest *Athenaegis* within the cyathaspids (Fig. 5B; Randle *et al.* 2025). Whatever the case, understanding of the polarity of feeding states within heterostracans (and the rest of the jawless ostracoderms) requires consideration of the diversity of conditions within the individual lineages and further refined models for oral plate homology and function within the group.

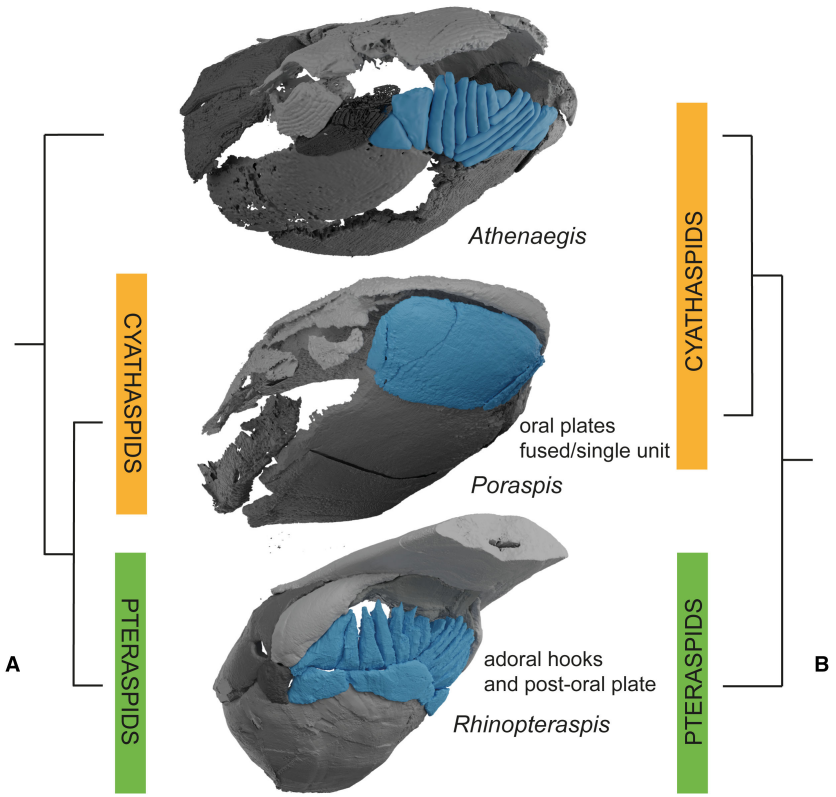


FIG. 5. Simplified summaries of alternate phylogenies featuring *Athenaegis*, *Poraspis* and *Rhinopteraspis*. A, based on Randle & Sansom (2017) with *Athenaegis* as a sister taxon to the cyathaspids and pteraspids. B, based on Randle *et al.* (2025) with *Athenaegis* nested within the cyathaspids. Partial reconstruction of *Athenaegis chattertoni* based on work herein, *Poraspis thomasi* based on specimen FMNH-PF14474, described and figured by Elliott & Petriello (2011, figs 2C, 4), *Rhinopteraspis dunensis* re-rendered from Dearden *et al.* 2024. Oral plates and postoral plates coloured blue.

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CONCLUSION

We present a revised reconstruction of the oral region of *Athenaegis*, the stratigraphically oldest heterostracan known from articulated body fossils and feeding apparatus. Our interpretation of the function of the oral apparatus in *Athenaegis* is consistent with previous hypotheses of suspension feeding in heterostracans. The oral region of *Athenaegis* was incapable of substantial opening due to the interdigitating oral plates and their tight articulation with the surrounding dermal elements, as well as the absence of any substantial muscle/ligament insertion points. The function of the oral plates appears to have been to constrain a dorsoventrally narrow opening to the mouth, with the gill arches presumably generating water flow through the head. *Athenaegis* also demonstrates variability within the structure of the oral region in heterostracans, displaying functional similarities to the single large oral plate of taxa such as *Poraspis* and morphological similarities to the multiple ' finger-like' oral plates of taxa such as *Rhinopteraspis*.

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DATA ARCHIVING STATEMENT

The synchrotron data collection is available via the ESFR portal (https://doi.org/10.15151/ESRF-DC-2017287792) and in MorphoSource: https://www.morphosource.org/projects/000711898 (scans of *Athenaegis chattertoni*: anterior body region (UALVP 39923), https://doi.org/10.17602/M2/M707917; posterior body region (UALVP 39923), https://doi.org/10.17602/M2/M708003; anterior body region (UALVP 29926), https://doi.org/10.17602/M2/M708110, https://doi.org/10.17602/M2/M708008; full body scan of the holotype (UALVP 15682), https://doi.org/10.17602/M2/M708016).

The three-dimensional models for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.9p8cz8wtb.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.70088):

Appendix S1. Figures S1–S4: additional specimen images (UALVP 29926, 33923, 15682) and retrodeformed reconstruction (UALVP 29926) of *Athenaegis chattertoni*.
Video S1. Video of the composite reconstruction of *Athenaegis chattertoni* based on UALVP 29926 and UALVP 33923, showing the hypothesized extent of oral apparatus movement from dextral, anterior, anterosinistral and anteroventral viewpoints.

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