Ex vivo three-dimensional reconstruction of *Acutiramus:* a giant pterygotid sea scorpion

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ABSTRACT

Pterygotid eurypterids include some of the largest aquatic arthropods in the fossil record and are known from middle Silurian to Middle Devonian deposits across the globe. These forms primarily preserve as mostly two-dimensional impressions, a situation that has impacted the accurate reconstruction of pterygotid ventral structures and organization. By documenting specimens displaying important dorsal and ventral structures from both *Acutiramus*—a larger, well-documented pterygotid genus—and other pterygotids, we reconstruct *Acutiramus* in three-dimensions (3D) to more thoroughly understand the functional morphology and limb arrangement of these large eurypterids. With this comprehensive 3D reconstruction, we demonstrate a much more anterior insertion of appendages II–V, a near-horizontal orientation of appendages II–VI coxae, the presence of reduced appendage II, and a labrum and epistomel region. The labrum and epistomel sections are identified as the locality for cheliceral articulation. This model also uncovers the streamlined nature and low-profile morphology of *Acutiramus*. We use our model to explore the morphofunctionality of pterygotid eurypterids, including their feeding strategies, addressing a conundrum inherent in previous pterygotid reconstructions.

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INTRODUCTION

Virtual paleontology has become an active field since the turn of the 21st century (Garwood et al., 2010; Abel et al., 2012; Rahman et al., 2012; Cunningham et al., 2014; Sutton et al., 2016). This reflects the more frequent application of methods like computed tomography that permit reconstruction of fossils in three dimensions (3D) (Hohenstein, 2004; Sutton, 2008; Scherf, 2013; Sutton et al., 2014; Johnson and Carter, 2019). These approaches have permitted the virtual dissection of fossils from rock or amber (Sutton, 2008; Perreau and Tafforeau, 2011) and the illustration of specimens in 3D (Cunningham et al., 2014; Jauvion et al., 2016; Lee et al., 2017)—a direction that is especially useful in documenting holotype material for global dissemination (Garwood et al., 2011; Garwood and Dunlop, 2014; Ashe-Jepson et al., 2019; Bicknell et al., 2022a). This expansion of virtual paleontology has also resulted in a synthesis between paleontology and 3D computational methodologies, such as fluid-dynamic and kinematic approaches (Rayfield, 2007; Anderson and Westneat, 2009; Cunningham et al., 2014; Brassey et al., 2017). Together, these developments have expanded how the morphology and ecology of fossil animals are understood and recorded.

Examining arthropods with virtual paleontology methods has become more common over the past decade. Most research in this context has scanned, dissected, and reconstructed arthropods in amber (e.g., Dunlop et al., 2011; Liu et al., 2017; Pérez-de la Fuente et al., 2019; Szabó et al., 2022). However, the virtual dissection of arthropods from other rock matrices has become more common for crustaceans (Eriksson et al., 2016; Jauvion et al., 2016, 2020), chelicerates (Garwood et al., 2011; Garwood and Dunlop, 2014; Lamsdell et al., 2020), anomalocarids (Wu et al., 2021), and other basal arthropods (Liu et al., 2015, 2016, 2020; Zhai et al., 2019; Jin et al., 2021). These virtual dissections are possible as specimens either are preserved in 3D or show a marked density difference between the fossil and the host matrix—conditions that allow for informative scans. Other approaches have involved sectioning fossils, digitizing the slices, and reconstructing the fossil in 3D from slice stacks. This has been used effectively for arthropods from the mid-Silurian (Homerian) Herefordshire Lagerstätte (Orr et al., 2000; Sutton et al., 2002; Briggs et al., 2004, 2012, 2016; Siveter et al., 2017, 2020). One final approach that has emerged is the ex vivo 3D reconstruction of arthropods preserved in conditions that are (1) not conducive scanning or sectioning (Haug et al., 2012; Bicknell et al., 2018b, 2021, 2022b; 2023; Schmidt et al., 2022; Lu et al., 2023), or (2) when the soft-bodied material is limited or completely lost due to preservation, as in trilobites (Esteve et al., 2017, 2018; Laibl et al., 2023). This approach builds on more traditional methods of constructing physical models to understand compressed arthropods (see Fisher, 1977; Briggs and Williams, 1981; Plotnick and Baumiller, 1988). This method is especially useful as distinct exoskeletal components can be reconstructed in isolation within a 3D framework, after which the different body parts can be pieced together for the complete model. Taking this approach, the entire animal and distinct components to be examined and digitally dissected.

One Paleozoic arthropod group worth considering with ex vivo reconstruction the sea scorpions (eurypterids). Recent ex vivo 3D reconstructions of eurypterids have focused on appendages to understand range of motion (Bicknell et al., 2022c; Schmidt et al., 2022) and

cheliceral biomechanics (Bicknell et al., 2022b). These reconstructions have been necessary as most eurypterids are preserved as near 2D impressions (although see examples of cuticular preservation in Holm, 1898, Selden, 1981, Lamsdell et al., 2015, and Bicknell et al., 2018b) and rare 3D preservation (Lamsdell et al., 2020). One eurypterid group that could be explored with these new 3D reconstruction approaches is the pterygotids—eurypterids that at the upper limits of their body size reached lengths in excess of 2.5 m (Braddy et al., 2008). The diagnostic feature of Pterygotidae is the greatly expanded chelicerae. These structures are far larger than those in any other eurypterid, even the closely related *Slimonia* Page, 1856 (Kjellesvig-Waering, 1964; Waterston, 1964). As such, there has been considerable research into these structures (see Kjellesvig-Waering, 1964; Waterston, 1964; Bicknell et al., 2022b), with the overall conclusion that they are used in predation.

The 2D preservation of nearly all pterygotid fossils has resulted in the superimposition of dorsal and ventral structures, impacting accurate reconstructions of ventral structures and their anatomical arrangement (Wills, 1966). To address this situation, we present a 3D reconstruction the pterygotid *Acutiramus* Ruedemann, 1935, informed through detailed examination of pterygotid specimens displaying unique anatomical details (available in the online supplement: https://doi.org/10.5531/sd.sp.61). Through this application of ex vivo 3D reconstruction, we uncover novel insights into the ventral organization of pterygotid appendages, explore the functional morphology of pterygotids, and discuss how our model differs from more traditional reconstructions.

Historical Reconstructions

The pterygotids *Pterygotus* Agassiz, 1844, and *Erettopterus* Salter in Huxley and Salter, 1859, were among the first named eurypterids and, therefore, the first to receive detailed monographic examination (Huxley and Salter, 1859). Pterygotids were known from numerous isolated fragments, with a few articulated molts (Tetlie et al., 2008). Because of this situation and the complexity of the phylogenetic relationships between eurypterids and chelicerates, homologies regarding pterygotid body parts rapidly emerged during the late 19th century (Huxley and Salter, 1859; Woodward, 1866–1878; Laurie, 1895). Early pterygotid reconstructions therefore varied widely, especially regarding appendage anatomy and organization of the ventral side (M'Coy in Lyell, 1855; Salter, 1856; Huxley and Salter, 1859; Murchison, 1859; Page, 1859; Woodward in Lyell, 1865; Woodward, 1866–1878; Schmidt, 1883). The canonical reconstruction of pterygotids was published by Clarke and Ruedemann (1912) and based on *Acutiramus cummingsi* (Grote and Pitt, 1877) (= *Pterygotus buffaloensis* in the older literature; fig. 1). This reconstruction was used in the *Treatise on Invertebrate Paleontology* (Størmer, 1955) and has been the reference reconstruction and representation in artwork over the past century (e.g., Augusta and Burian, 1958; Ciurca and Tetlie, 2007; Braddy et al., 2008; Tetlie and Briggs, 2009; Naugolnykh and Shpinev, 2018; Swaby et al., 2022). However, there are key aspects of the appendage reconstruction and arrangements in figure 1 that require critical reassessment:

1. The chelicerae are three jointed, with the proximal podomere longer than the chela.

2. The chelicerae attach medially, but project laterally at the median margin of the large compound eyes.

3. Appendages II–V are approximately the same size, with appendage II slightly reduced compared to appendages III–V.

4. Appendages II–V extend laterally anterior to the coxa of appendage VI ("swimming legs" of Plotnick, 1985) and project along the lateral prosomal region.

We demonstrate here that points 2–4 are incorrect and need a more accurate representation.

INSTITUTIONAL ABBREVIATIONS

AMNH-FI: Fossil invertebrate collection, American Museum of Natural History, New York. **BMS:** Buffalo Museum of Science, Buffalo, NY. **NHMUK PI:** Invertebrate palaeontological collection, Natural History Museum, London, UK. **NYSM:** New York State Museum, Albany, NY. **USNM:** National Museum of Natural History (U.S. National Museum), Washington, DC. **YPM IP:** Yale Peabody Museum Invertebrate Paleontology collection, New Haven, CT.

METHODS

To inform the reconstruction, we examined new photographs of *Acutiramus* specimens. The majority of specimens were housed within the AMNH-FI, BMS, NHMUK PI, NYSM, USNM, and YPM IP collections. Additional specimens from Lang's Fossils (Ilion, NY) were also considered. Finally, we employed published high-resolution images of *Acutiramus* and other pterygotids (Waterston, 1964; Chlupáč, 1994; Tetlie and Briggs, 2009; Laub et al., 2010; Bicknell et al., 2022b). Fossils that illustrate key aspects of the morphology are shown in figures 2–7.

The 3D reconstruction of *Acutiramus* was rendered in Zbrush (Pixologic, Inc). The model construction started with a series of simple shapes that were manipulated into the generalized *Acutiramus* morphology and then more finely sculpted in an additive and reductive process. This process resulted in over 30 model versions to produce the final reconstruction. The final version reflected detailed scrutiny of the scale and size of exoskeletal regions of specimens and aligning the model with specimen images. The process of building the animal section by section also allowed us to pinpoint more precisely where in 3D space the ventral morphologies should be positioned. The degree of exoskeletal "inflation" for this finalized model was informed by examining eurypterid specimens preserved in 3D (e.g., Lamsdell et al., 2020), and specimens of *Erettopterus osiliensis* (Schmidt, 1883) in the NYSM collection. This approach was needed as there is very limited density difference between pterygotid fossils and the host matrix (Bicknell et al., 2022c). As a result, scanning these fossils would have produced unreliable 3D data; our model circumvents this core limitation of the pterygotid fossil record. Reconstructions were exported as .stl files from Zbrush and imported into Geomagic (3D Systems) where the models were scaled to the size of the *Acutiramus* chelicerae analyzed in Bicknell et al. (2022b). After scaling, .stl files were exported from Geomagic and imported into Tetra4D to generate a 3D pdf.
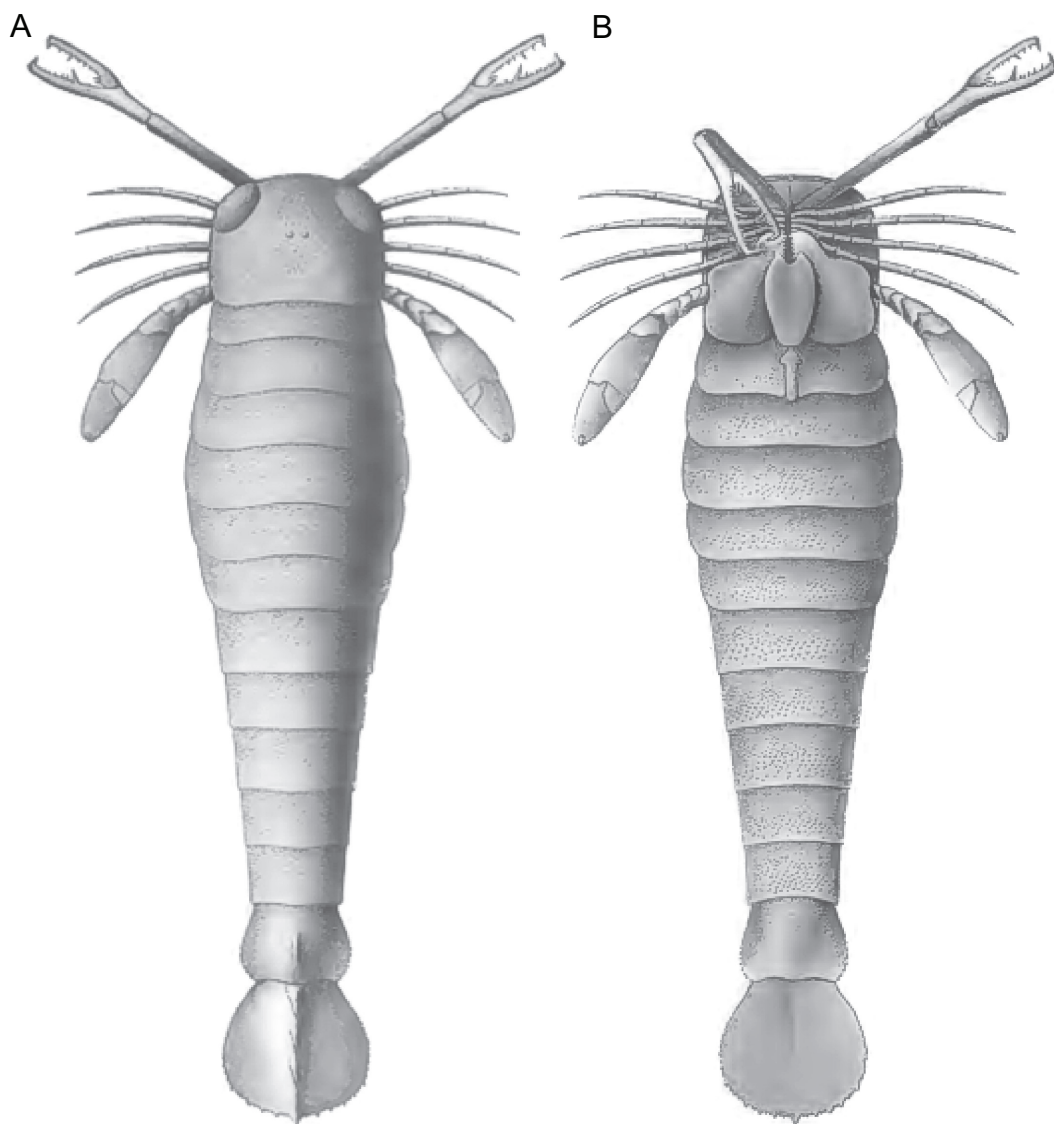
FIGURE 1. The traditional reconstruction of *Pterygotus* from Clarke and Ruedemann (1912: pls. 67, 68): **A.** dorsal reconstruction; **B.** ventral reconstruction.

RESULTS

Examination of *Acutiramus* and other pterygotid specimens clarified the nature, orientation, and position of ventral structures. These observations were critical to producing the 3D reconstruction and highlighted issues with the Clarke and Ruedemann (1912) interpretation. In light of the numerous cheliceral specimens we examined (e.g., figs. 2B, D, 3, 5), we confirmed the presence of three podomeres (cf. Kjellesvig-Waering, 1964) and that the proximalmost podomere is longer than the chelae. Moreover, the proximalmost podomere shows
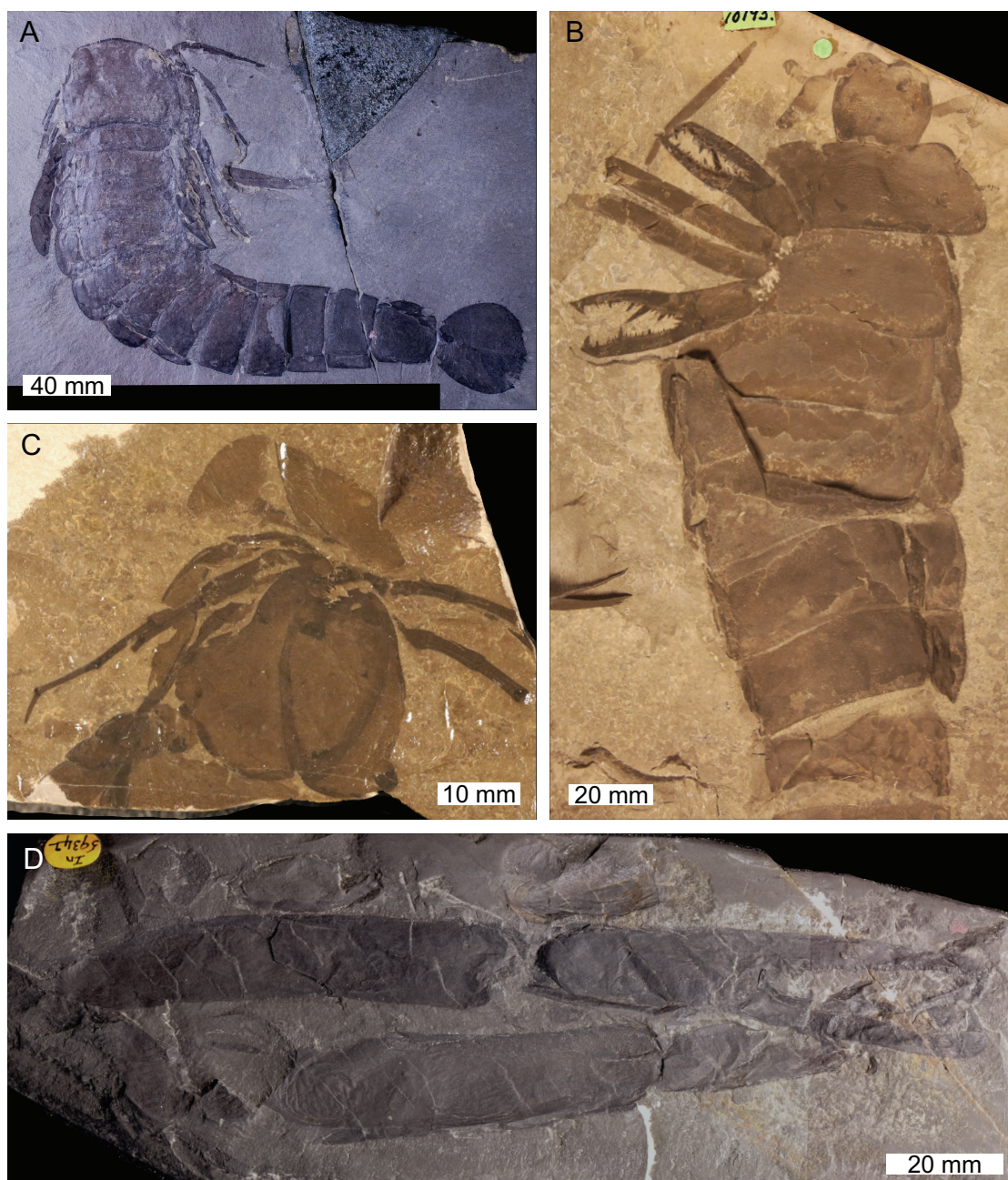
FIGURE 2. *Acutiramus* and *Erettopterus* specimens showing the general morphology and arrangement of appendages and ventral structures. **A, B.** *Acutiramus cummingsi* from the Silurian (Pridoli), Bertie Group, Williamsville Formation, Bennett Quarry (= Buffalo Cement Company), Buffalo, NY (N 42.942, W 78.825). **A.** USNM PAL 60053 (Clarke and Ruedemann, 1912: pl. 72, fig. 1). **B.** NYSM 10193 (Clarke and Ruedemann, 1912: pl. 78, fig. 3). **C.** *Acutiramus macrophthalmus* (Hall, 1859) from the Silurian (Pridoli), Bertie Group, Fiddlers Green dolomite. No locality data. NYSM E3584. **D.** *Erettopterus bilobus* (Salter, 1856) from the Silurian (latest Llandovery and Wenlock) Patrick or Kip Burn formation, Scotland. NHMUK PI In 59342. **A–C.** Photographed under water. **B, C.** Photographs by Lisa Amati.

marked tapering proximally, suggesting a much-reduced articulation area at the proximal region (fig. 3A, C; see below). Further, a nearly complete specimen (YPM IP 208195; fig. 7) illustrates the possible chelicerae-prosoma articulation region. The anterior margin of the specimen shows an epistoma anterior to structures we interpreted as the epistome and labrum, similar to *Limulus* Müller, 1785 (Snodgrass, 1952). The chelicerae would likely have articulated with the epistome, lateral to the prosomal medial line.

The similarity in spelling between *epistome* and *epistoma* has caused confusion in the literature. Following the usage by Størmer (1934), the *epistoma* is the median plate of the doublure (figs. 5–7), separated from the lateral shields by epistomal sutures (figs. 5–7). In contrast, using Snodgrass (1952), the *epistome* is the plate that continues posteriorly to the labrum, ventral to the mouth and is the locality for cheliceral articulation (fig. 7).

A key specimen for understanding ventral arrangement was described by Kjellesvig-Waering (1964: pl. 53, fig. 1, text-fig. 11), who also presented possible evidence of a chelicera articulating with the "anterior part of the ventral shield" (fig. 5). Reexamining this specimen, we conclude that it is a fragmentary, disarticulated specimen with an isolated prosomal appendage (likely appendage III) and the so-called ventral shield is the epistoma and associated lateral shields (cf. Clarke and Ruedemann, 1912: pl. 71, fig. 3; Størmer, 1934). The preserved proximal cheliceral region is located along the epistomal midline, precluding any space for the second chelicera. Furthermore, the chelicera is truncated proximally, suggesting the chelicera is overlain by the epistoma. As such, the specimen represents a chance association, and not an accurate record of the proximal cheliceral articulation.

Appendages II–V insert within the first third of the prosoma and splay anteriorly relative to the compound eye, as opposed to laterally (figs. 2A, 2C, 4). Specimens preserving appendage II demonstrate that the appendage is significantly reduced compared to appendages III–V (figs. 4, 7). This mirrors the reduced appendage II size in *Erettopterus* (Selden, 1986), *Ciurcopterus* Tetlie and Briggs, 2009, and *Slimonia* (Lamsdell, 2022: fig. 5). *Acutiramus* therefore had three sets of "walking legs" and a pair of reduced palps.

Appendage II coxae have been considered either fused with the labrum to form an infracapitulum (sensu Selden, 1986), or fused with the ventral shield (sensu Kjellesvig-Waering, 1964: pl. 53, fig. 1). However, the labrum and appendage II coxae have been illustrated as distinct structures (Haug, 2020: fig. 5b) and examination of *Acutiramus macrophthalmus* has illustrated that appendage II coxae are unfused (fig. 4C). They are located proximal, and anterior to the oral groove. This results in reduced, anterolateral orientated appendages (figs. 4, 6). Related to this, the specimen identified by Selden (1986) as *Erettopterus* (fig. 6) is likely an example of the epistoma and lateral shields of *Slimonia*, with an attached reduced appendage II, including the coxa (Lamsdell, 2022).

Based on these data, our 3D reconstruction of *Acutiramus* uncovered a complex arrangement of ventral structures (figs. 8, 9, supplemental fig. 1). Due to the limited prosomal inflation, coxal sections of prosomal appendages must have been orientated more horizontal than vertical, contrasting with the condition in xiphosurids (Bicknell et al., 2018c). This orientation permits the metastoma to be flush with appendage VI coxae. Anterior to appendage VI were
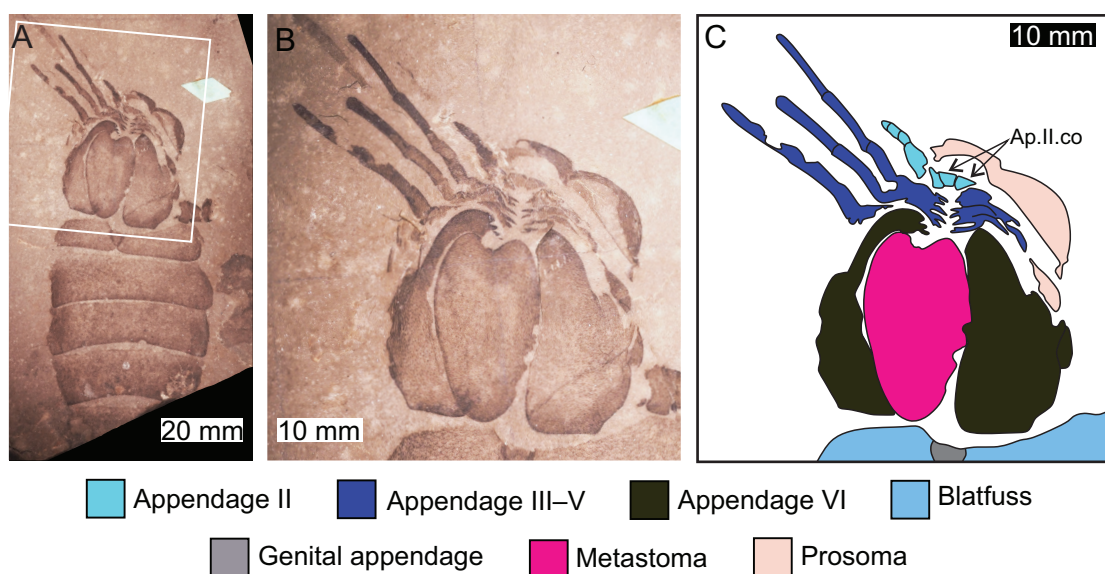
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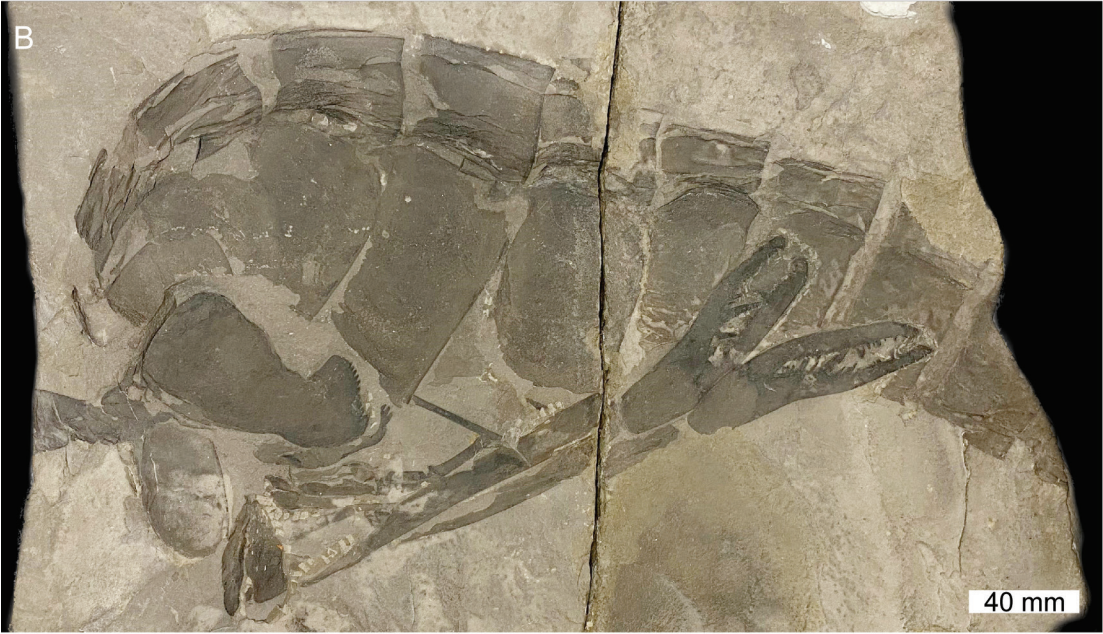
FIGURE 4. *Acutiramus macrophthalmus* showing arrangement of ventral structures. AMNH-FI 2253; specimen from the Silurian (Pridoli), Bertie Group, Waterville, Oneida County, NY (Clarke and Ruedemann, 1912: pl. 71, fig. 6): **A.** complete specimen; **B.** close-up of ventral structures; **C.** interpretive drawing of B. Abbreviation: **Ap.II.co,** appendage II coxae. Specimens photographed under ethanol.

the appendages II–V that are arranged anteriorly and insert within the first third of the prosoma. Appendage II is reduced in size compared to appendages III–V. Anterior to these appendages are the labrum and epistome. We consider the epistome, labrum, and appendage II coxae distinct structures. The hypertrophied chelicerae consisting of three podomeres taper proximally and insert laterally within the labrum and epistomel region, close to the longitudinal axis of the body, directed anteriorly, and extending well beyond the prosoma. Rotating the moveable and fixed cheliceral rami about the primary cheliceral articulation demonstrates that raptorial chelicerae could have moved prey captured with the appendages to the ventral region for processing.

DISCUSSION

Pterygotid chelicerae were undoubtedly used to capture prey for processing by coxal gnathobases (Waterston, 1964; Miller, 2007; Bicknell et al., 2022b). This predatory ecology is further supported through correlations between chelicerae and lateral compound eye shapes (Anderson et al., 2014; McCoy et al., 2015) and 3D biomechanical analyses (Bicknell et al., 2022b). For *Acutiramus* specifically, species of this genus have serrated, oblique, elongated, anteriorly directed, denticles

FIGURE 3. Examples of *Acutiramus cummingsi* chelicerae. **A.** YPM IP 545056 from the Late Silurian (Pridoli), Bertie Group; Williamsville Formation, Ridgemount Quarry South, Bertie Township, Welland County, Ontario, Canada (N 42.913 W 79.005). **B, C.** Specimens from the Late Silurian (Pridoli), Bertie Group, Williamsville Formation, Bennett Quarry, Buffalo, NY. **B.** BMS E845 (Clarke and Ruedemann, 1912: pl. 74). **C.** YPM IP 018609. **A, C.** Photographs by Jessica Utrup.
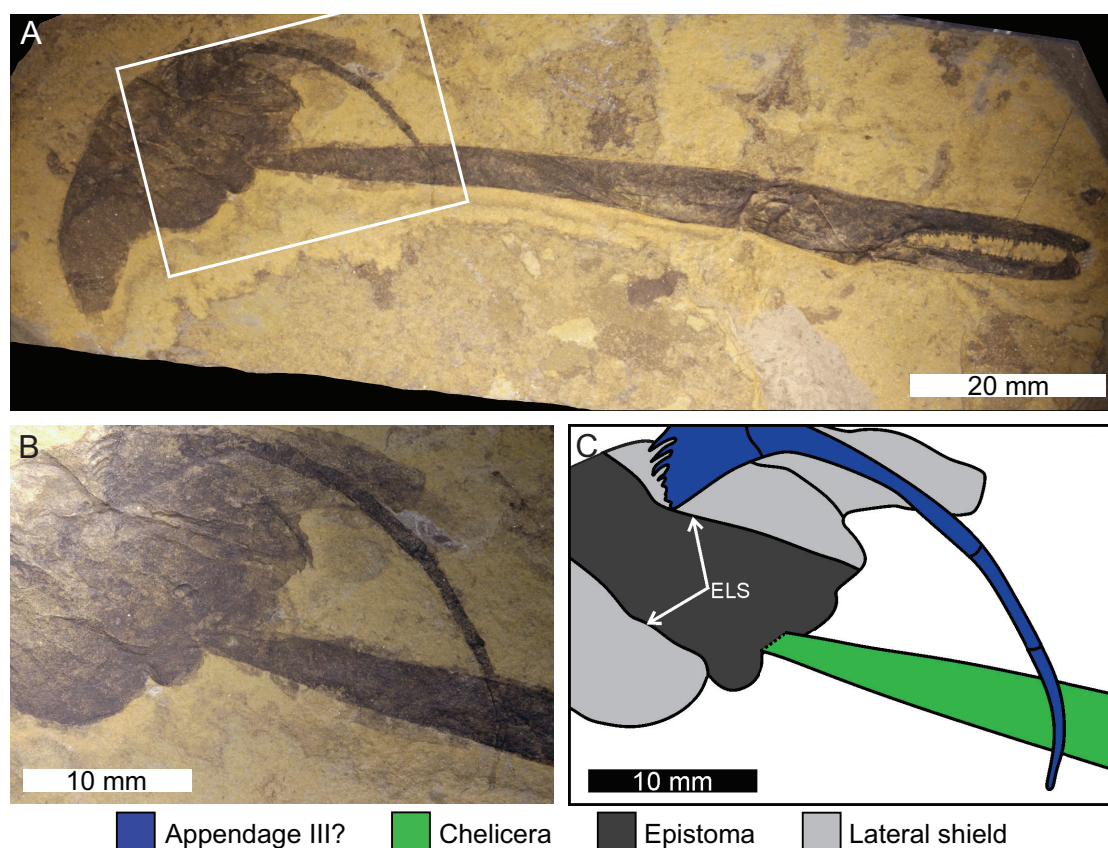
FIGURE 5. *Erettopterus bilobus* from the Silurian (latest Llandovery and Wenlock) Patrick or Kip Burn forma-
tion, Scotland. NHMUK PI In 59343 (Kjellesvig-Waering, 1964: pl. 53, fig. 1): **A.** complete specimen; **B.** close-
up of rectangle in A showing the purported cheliceral articulation with the epistoma; **C.** interpretive drawing
of B showing the reduction in cheliceral width proximal to the epistoma. Abbreviation: **ELS,** epistomal lateral
sutures. Specimen photographed under ethanol.

(Chlupáč, 1994; Laub et al., 2010; McCoy et al., 2015; Bicknell et al., 2020). These morphologies are
poorly adapted to capturing armoured or thick-shelled prey (Laub et al., 2010; Bicknell et al., 2022b).
As such, they would likely have been more effective in piercing the thin cuticle of cooccurring
eurypterids (Laub et al., 2010; Anderson et al., 2014; Bicknell et al., 2022b), phyllocarids (Collette
and Plotnick, 2020), or soft-bodied organisms; impaling prey for subsequent processing (Laub et
al., 2010), similarly to other proposed apex predators (see Bicknell et al., 2023).

The size and podomere number for pterygotid chelicerae has created difficulties in under-
standing how pterygotids moved food from the chelicerae to the oral region. Kjellesvig-Waer-
ing (1964) suggested that three podomeres would have limited the ability for chelicerae to move
prey directly to the gnathobasic region for processing and discounted the use of appendages
II–V in manipulating food items. Instead, he proposed an additional joint along podomere 1
and supported this with figures of *Erettopterus* and *Acutiramus*. This additional joint allowed
for increased range of motion. However, reconsiderations of this same *Erettopterus* material
has demonstrated (1) the presence of a tendon along the first podomere (Selden, 1984) and (2)

that the inferred articulation was a crack (Laub et al., 2010). We have found no evidence for four-segmented chelicerae (figs. 2D, 3, 5). We therefore reject the proposal of an additional podomere and have reconstructed chelicerae with three podomeres.

The chelicerae are reconstructed here as inserting proximal to the longitudinal axis and tapering proximally to the body. This reflects those rare cheliceral specimens that show a tapered proximal section of podomere 1 (figs. 2B, D, 3B, C, 5) and the proposal that chelicerae articulate proximal to the epistome and labrum, similar to xiphosurans (Snodgrass, 1952; Budd, 2021). Furthermore, we determine that there is limited space for a larger cheliceral articulation (fig. 7C). The proximal taper and ventral articulation suggest that the chelicerae were capable of a wide range of movement, resulting in a ball-in-socket-like joint.

The reduced proximal articulation, as modeled here, presents a conundrum—the chelicerae may have been disarticulated by a struggling prey item. Furthermore, as the chelicerae were used in predation, one might expect a reinforced and robust articulation. One possible explanation is that these arthropods had a specialized, soft-bodied diet (Hays et al., 2018). Alternatively, large muscles may have emerged from the triangular proximal portion of the first podomere, providing a robust attachment. However, this condition would have reduced the cheliceral mobility. One final option is that surrounding the articulation there was a large volume of arthrodial membrane that is not preserved. This would have allowed for reinforcement without decreasing mobility. Ultimately, a fortuitously preserved corpse should muscle groups and the cheliceral articulation is needed to unambiguously address this situation.
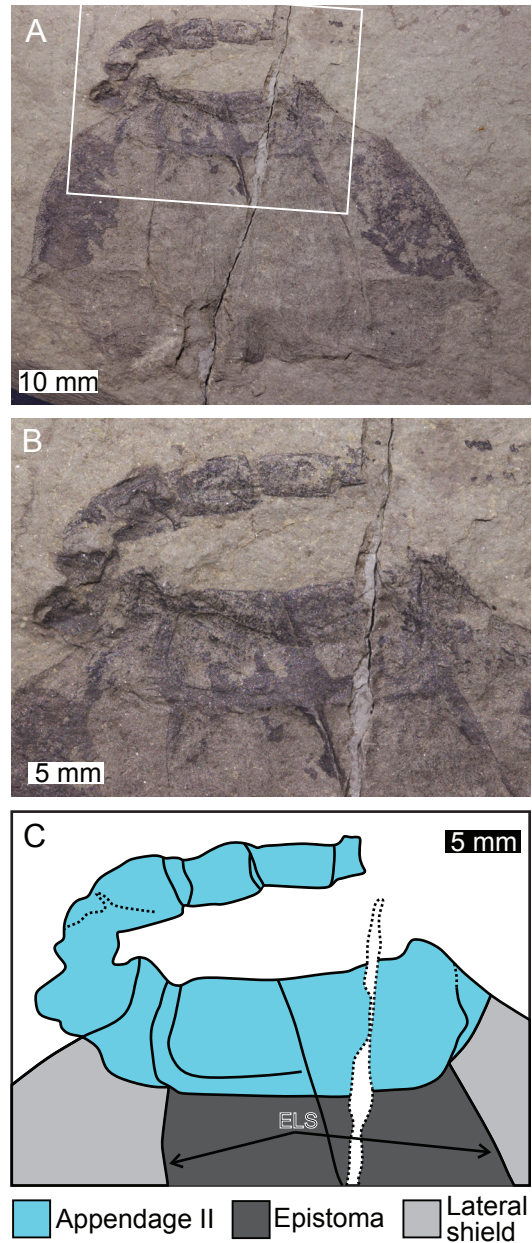

FIGURE 6. *Slimonia acuminata* (Salter, 1856) from the Silurian (latest Llandovery and Wenlock) Patrick or Kip Burn formation, Scotland showing epistoma and the reduced appendage II. NHMUK PI 59651 (Selden, 1986: text-fig. 1B): **A.** complete specimen; **B.** close-up of rectangle in A showing the reduced appendage II; **C.** interpretive drawing of B. Abbreviation: **ELS,** epistomal lateral sutures. Specimen photographed under ethanol.
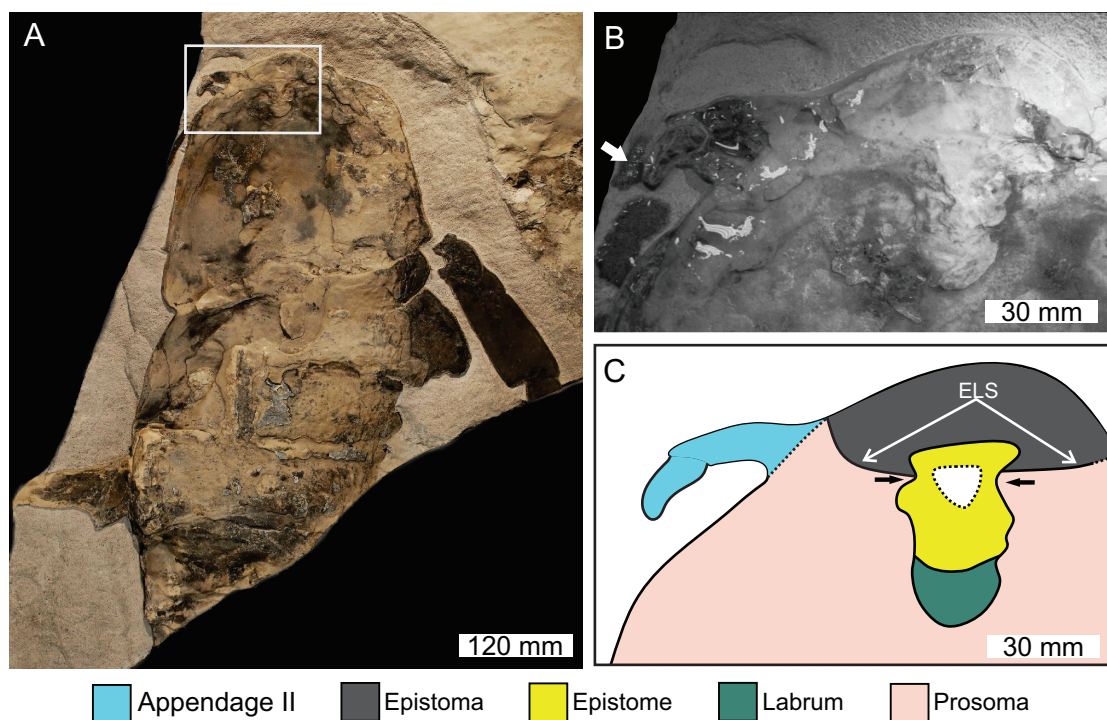
FIGURE 7. *Acutiramus macrophthalmus* showing ventral morphology. YPM IP 208195 from the Late Silurian (Pridoli), Bertie Group, Fiddlers Green dolomite, Phelps Waterline Member, SW of Spinnersville, Millers Mills Quadrangle, Herkimer County, NY (Briggs and Roach, 2020: figs. 10, 11): **A.** complete specimen. **B.** close-up of rectangle in A showing reduced appendage II (white arrow); **C.** interpretive drawing of close-up in B showing key morphologies and the possible articulation locality for the chelicerae (black arrows). B converted to grayscale. Abbreviation: **ELS,** epistomal lateral sutures. **A, B.** Photographs by Jessica Utrup.

We reconstructed the chelicerae as anteriorly directed (figs. 8A, C, 9A). This reflects a proposed, attacklike orientation where the chelicerae function with the anteriorly located lateral compound eyes to identify and capture prey (Anderson et al., 2014; McCoy et al., 2015). This outstretched condition is likely hydrodynamically optimized for predation (see analyses on raptorial appendages in Bicknell et al., 2023). However, maintaining this orientation would likely have been energy intensive. As such, this orientation would not have been observed at all points in life. It is possible that while moving passively through the water, the animal may have rotated the chelicerae ventrally, akin to harvestmen prosomal appendages (Wolff et al., 2016), or rotated the hypertrophied chelicerae sagittally, akin to scorpion pedipalps in a defensive, withdrawal posture (Palka and Babu, 1967). Range-of-motion and fluid-dynamic analyses are needed to confirm these suggestions. While this was far beyond the scope of our study, they represent interesting new directions to further the understanding of pterygotid paleobiology.

The so-called walking legs have previously been reconstructed as eight, laterally splayed appendages that insert along the prosoma (Clarke and Ruedemann, 1912; Braddy et al., 2008; Laub et al., 2010). *Acutiramus* has been reconstructed standing on "walking legs" with the telson and metasoma deflected dorsally, comparable to a scorpion in a defensive stance
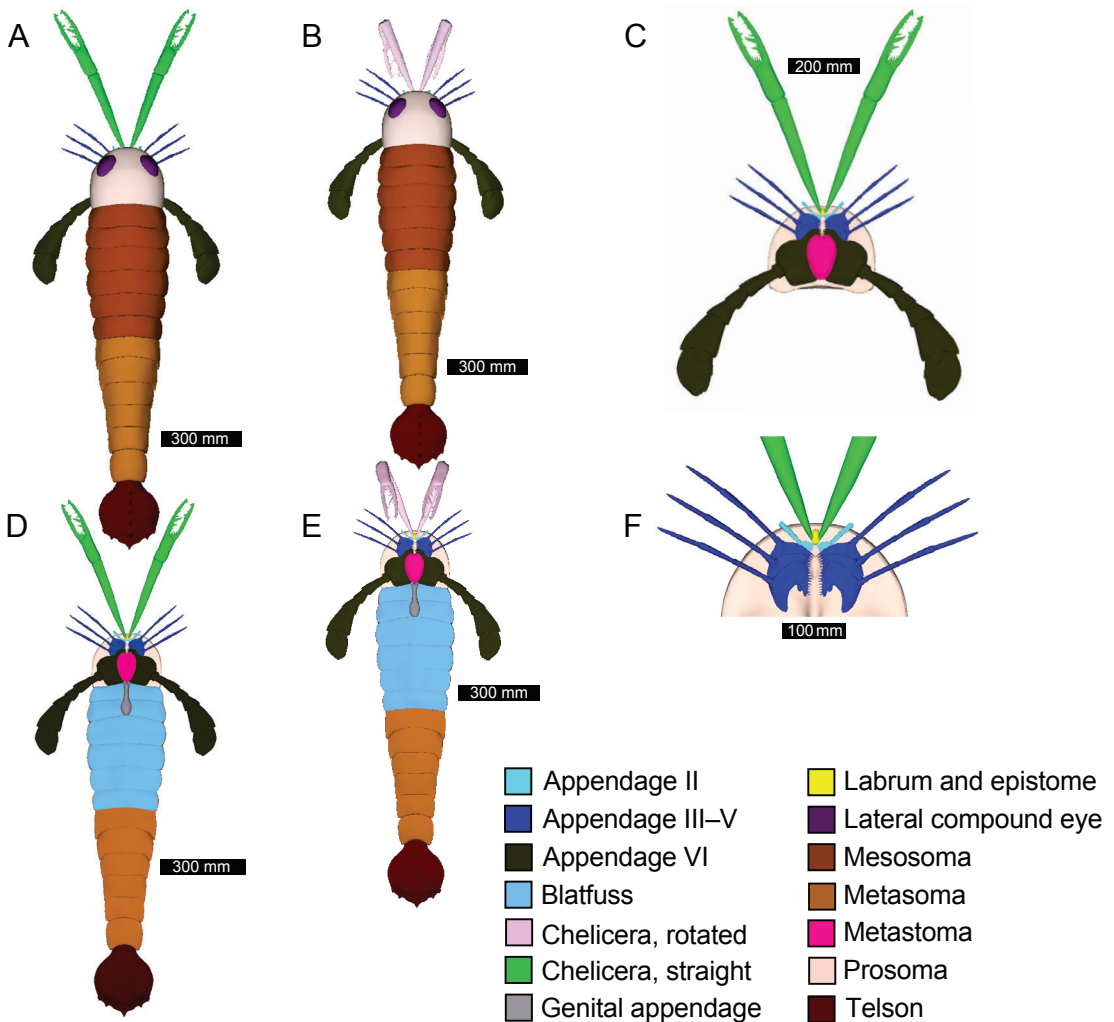
FIGURE 8. 3D reconstruction of *Acutiramus* based on examined specimens in dorsal and ventral view. **A, D.** Reconstruction with chelicerae outstretched: **A.** dorsal view; **D.** ventral view. **B, E.** Reconstruction with chelicerae rotated: **B.** dorsal view; **E.** ventral view. **C, F.** Close-up of prosomal region in ventral view: **C.** all prosomal appendages; **F.** close-up of appendages II–V with appendages VI and metastoma removed. The 3D pdf associated with this reconstruction, figure S1, is available in the online supplement (https://doi.org/10.5531/sd.sp.61).

(Coelho et al., 2017). Instead, we demonstrate that appendages II–V insert and are arranged anteriorly, with appendage II reduced in size. The reduced size of appendage II and thin nature of appendages III–V would have limited their use in benthic locomotion (Waterston, 1964). These morphologies, combined with a more anterior orientation, would have limited overall balance, decreasing the use of these structures in walking. It is possible that if pterygotids rested on the bottom, they could have balanced using appendage VI paddles and the laterally expanded telson. Taken together, we propose a much more pelagic to nektobenthic life mode for these large chelicerates (Clarke and Ruedemann, 1912; Waterston, 1964; Plot-
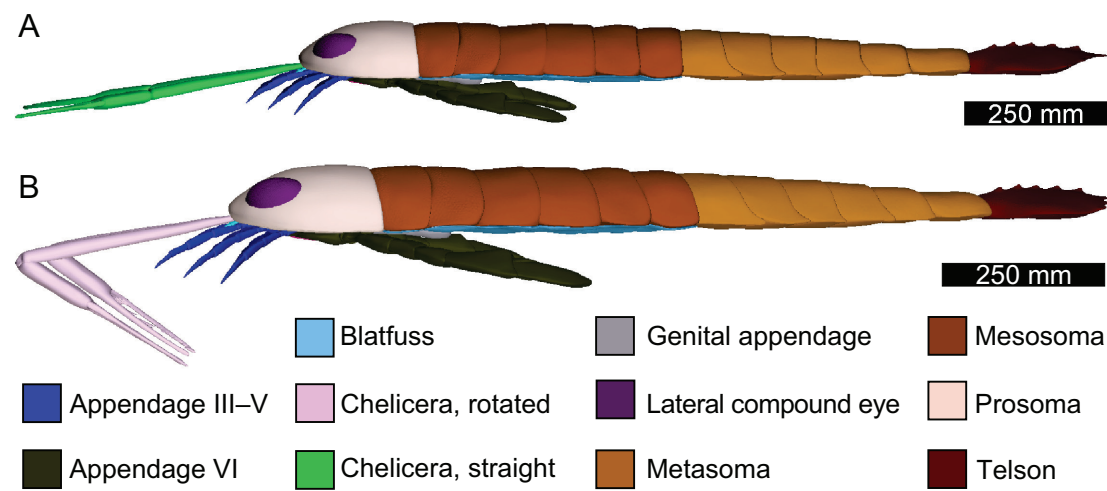
FIGURE 9. 3D reconstruction of *Acutiramus* based on examined specimens in lateral view. **A.** Reconstruction with chelicerae outstretched. **B.** Reconstruction with chelicerae rotated. The 3D pdf associated with this reconstruction, figure S1, is available in the online supplement (https://doi.org/10.5531/sd.sp.61).

nick and Baumiller, 1988; Braddy and Gass, 2023), with limited time spent on the sea floor processing prey.

With the limited application in walking, it is important to consider the use of appendages II–V. We propose that they functioned in coordination with chelicerae to move prey items to the oral region, akin to scorpion walking legs (Bub and Bowerman, 1979). Food that was captured by the chelicerae would have been transferred to appendages III–V. These appendages would work in conjunction with the reduced appendage II to direct food items towards the gnathobasic spines for processing (Haug, 2020). This interpretation differs greatly from previous reconstructions that presented limited insight into how prey items may have moved from the chelicerae for processing by coxal gnathobases (Kjellesvig-Waering, 1964; Laub et al., 2010). This also suggests that appendages that are traditionally considered "walking legs" were repurposed for these large chelicerates.

A core limitation with the reconstruction presented here is that different specimens from different species were needed to construct the model. As such, we are unable to explore the full range of morphological variation within *Acutiramus* and report an idealized depiction of the genus. We propose that future examination of the pterygotids using 3D tools could therefore consider the morphological range at the species level to document possible dimorphism or differences in exoskeletal morphology.

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