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RAPID COMMUNICATION

Negative ontogenetic allometry of cardinal spines in the early Cambrian arthropod *Isoxys volucris* indicates their defensive function

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Abstract: The characteristic cardinal spines of *Isoxys*, a cosmopolitan bivalved arthropod, have been focal to understanding its role in Cambrian ecosystems. It has been proposed that the spines had either a hydrodynamic function, to aid buoyancy, or a defensive function, to protect against predators. Here, we demonstrate that the unusually elongated cardinal spines in *Isoxys volucris* (by far the most abundant taxon in the lower Cambrian Sirius Passet Lagerstätte, North Greenland) had a primary defensive function. Spine measurements of 85 specimens show a negative allometry during ontogeny, with the ratio of cardinal spine length to carapace length decreasing from >3.2 to 0.9. Negative allometric growth is inconsistent with a hydrodynamic function since larger carapaces would require spines which are proportionally at least as long (isometry or positive allometry). Instead, the negative allometry provides evidence for a defensive adaptation comparable to that seen in modern lower-trophic organisms, in which elongated spines increase the overall size of juveniles to deter predators. *Isoxys volucris* was the dominant food source for higher-trophic benthic and pelagic predators in the Sirius Passet biota, as revealed by the gut contents of arthropods, lobopods, palaeoscolecids and stem-chaetognaths. Its long spines therefore indicate similar adaptive responses to extremely high predation pressures in both modern and early Cambrian ecosystems.

Key words: *Isoxys*, negative allometry, defensive spines, gut contents, Cambrian food web, Sirius Passet.

ISOXYS is a common nektonic genus of bivalved arthropods in lower and middle Cambrian Burgess Shale-type Lagerstätten (Williams *et al.* 1996; Vannier & Chen 2000) and was an important member of the burgeoning early pelagic realm (Vannier & Chen 2000; Vannier *et al.* 2009; Pates *et al.* 2021). It is characterized by well-defined anterior and posterior cardinal spines which show great disparity in morphology and size (e.g. Vannier & Chen 2000; Pates *et al.* 2021), prompting debate about their function (Vannier & Chen 2000; Pates *et al.* 2021; Ma *et al.* 2023). According to one hypothesis, they functioned to create lift and drag to aid vertical swimming, with varying efficacy depending on their morphology (Pates *et al.* 2021). However, an alternative interpretation is that they had a primarily defensive function (Vannier & Chen 2000; Ma *et al.* 2023). This inference was originally proposed based on morphological comparisons with modern pelagic crab larvae (zoea) (Vannier & Chen 2000) which possess similarly long spines that are used to deter predators (Morgan 1989). It has recently been corroborated by an ontogenetic analysis of *I. minor* from the Qingjiang Lagerstätte (Ma *et al.* 2023), which showed a decrease in the length of its cardinal spines relative to carapace length (i.e. a negative allometry) of 18.4% to 7.8% (anterior spine, n = 36) and from 5.6% to 2.6% (posterior spine, n = 31). While *I. minor* possesses relatively short cardinal spines, *I. volucris* from the lower Cambrian Sirius Passet Lagerstätte (North Greenland) possesses notably elongated spines (Williams *et al.* 1996), with a needle-like morphology (Fig. 1) highly reminiscent of the long spines on some crab zoea (Morgan 1989). Consequently, their exaggerated condition provides an

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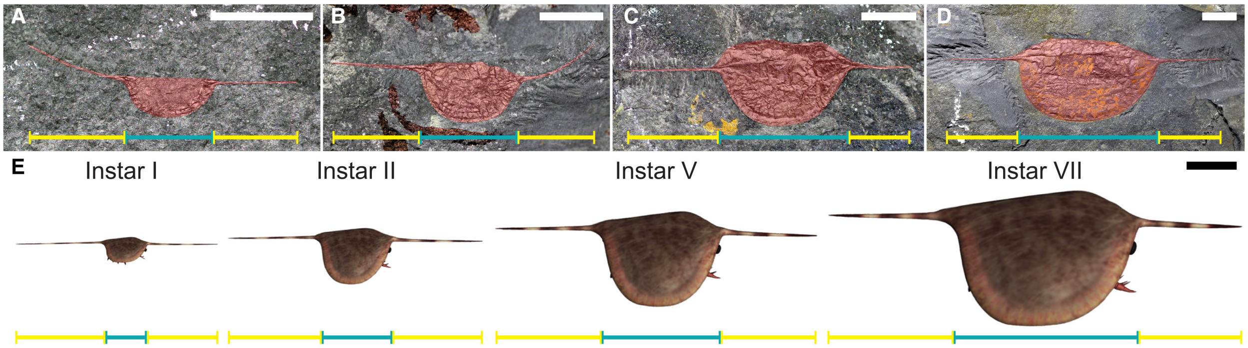

FIG. 1. Ontogenetic sequence of *Isoxys volucris* from Sirius Passet revealing negative allometry in spine length relative to carapace size. Blue bars illustrate carapace lengths, yellow bars cardinal spine lengths. A–D, representative stages in ontogenetic sequence; a transparent, red overlay has been added to the fossils to make their outlines more readily seen. E, digital reconstruction of *Isoxys volucris* with possible growth instars based on our dataset (see Results), artwork by Bob Nicholls. Accession numbers: A, MGUH 34832, mirrored photograph; B, MGUH 34833, mirrored photograph; C, MGUH 34834; D, MGUH 34835. Scale bars represent 5 mm.

ideal opportunity to test the opposing hypotheses and to resolve their purpose with greater certainty.

Isoxys volucris is by far the most abundant fossil in the Sirius Passet Lagerstätte, where it comprises 55% of all recorded fossils across the entire fossiliferous interval (Hammarlund *et al.* 2019; Harper *et al.* 2019) and up to 85% at certain levels. It often occurs as gut contents within other taxa, such as arthropods, palaeoscolecids and stem-chaetognaths (Peel 2017; Park *et al.* 2024), corroborating its trophic importance in both the biota's pelagic and benthic food webs. It has been interpreted to have been nektonic based on its carapace morphology (Williams *et al.* 1996) and on its long, paddle-shaped exopods (Stein *et al.* 2010), which it shares with other *Isoxys* taxa (Vannier & Chen 2000; García-Bellido *et al.* 2009a; Zhang *et al.* 2023). *Isoxys volucris* displays high intraspecific morphological variability, including considerable variation in cardinal spine length (Fig. 1A–D). While a size variation in the doublure width of the carapace has been shown to be unrelated to ontogeny (Nielsen *et al.* 2017), the nature of the observed variation in the length of its spines has yet to be investigated. In this study, we demonstrate a strong negative allometry for the cardinal spines of *I. volucris*, evidencing their primary defensive function.

MATERIAL & METHOD

The specimens analysed herein (Table S1) were collected during the 2016, 2017 and 2018 expeditions to Sirius Passet, Peary Land, North Greenland, led by the Korean Polar Research Institute (KOPRI). The Sirius Passet Lagerstätte is part of the Buen Formation, where the exceptionally preserved fossils occur in intervals of platy, laminated mudstones (Ineson & Peel 2011; locality 1 in Peel & Ineson 2011). The analysed specimens derive from many different horizons within these fossiliferous intervals.

Specimens analysed are currently part of the research collection at KOPRI, Incheon, South Korea but will be accessioned to the Natural History Museum of Denmark, Copenhagen, Denmark. Specimen numbers refer to the type collection numbers of the Natural History Museum of Denmark (MGUH) and field numbers used at KOPRI (B- or SP-prefix).

To assess spine allometry, we analysed the ratio between total spine length and carapace length in 85 articulated specimens of *I. volucris*. Total spine length is the sum of the posterior and anterior spine lengths. Carapace length is the length along the dorsal hinge line from the posterior to anterior ends of the doublure and therefore exclude the spines (see also Nielsen *et al.* 2017). Specimens were measured digitally from photographs using ImageJ software (Schneider *et al.* 2012) and linear regression of the data was performed in PAST v4.12 (Hammer *et al.* 2001) using its ordinary least squares-algorithm.

Photographs are of specimens either submerged in water under high-angle lighting to enhance contrast, or dry with a magnesium coating under low-angle lighting to enhance relief. Mirrored photographs, to display a consistent orientation of specimens, are indicated.

Predatory taxa containing specimens of *I. volucris* were photographed and digitized to highlight their gut contents. *Isoxys volucris* is distinguished from surrounding digested material because of the comparatively high relief of its sclerotised carapace, which is rare amongst taxa from Sirius Passet. Even so, estimates of abundances will constitute a minimum because of difficulties with definitively identifying highly comminuted and/or digested material. The density of specimens in a single specimen of *Pambdelurion whittingtoni* (MGUH 34836) was too high to confidently resolve every individual. So, for this specimen, we present both a low estimate, based on specimens with distinguishable diagnostic characters (e.g. carapace doublures and spines), and a high estimate, based on more effaced carapace outlines, partly obscured by overlapping superposition.

RESULTS

Total cardinal spine length ranges between 4.9 and 22.9 mm (mean 15.7 mm) and carapace length ranges between 2.6 and 20.3 mm (mean 10.8 mm), with total lengths (i.e. cardinal spines plus carapace) of the specimens ranging between 7.5 and 40.7 mm (mean 26.5 mm).

Ratios of cardinal spine length to carapace length show a strong negative allometry, with relative cardinal spine length consistently decreasing with increasing absolute carapace length (Fig. 2; $R^2 = 0.78$). The smallest specimens (<4 mm carapace length) have spines up to 3.2 times the length of their carapaces, while the largest specimens (>18 mm carapace length) have spines that are as little as 0.9 times the length of their carapaces. In the most extreme case (excluded from the study because its spines were not completely preserved), total spine length was 3.8 times that of the carapace (4 mm carapace length). Relative spine lengths fall into seven apparent plateaus, plausibly reflecting growth instars (Fig. 2).

DISCUSSION

The strongly negative allometry of cardinal spines documented here for *I. volucris* is inconsistent with a primary hydrodynamic function. Adult specimens would require proportionally at least as long cardinal spines as their juvenile counterparts to retain the streamlining effect that aids swimming or, more likely, require a positive allometry to counteract the accompanying hydrological shift in Reynolds' number (Ma *et al.* 2023). Consequently, a spine growth rate equal to (isometry) or higher than (positive allometry) the carapace growth rate would be expected.

Instead, the strongly negative allometry of cardinal spines is more consistent with a defensive function. Comparable negative spine allometries are documented from a range of modern animals, such as porcelain crab zoea (Morgan 1989), daphnids (Dodson 1984), rotifers (Gilbert 2018) and catfish (Fine *et al.* 2014). Long spines have been shown to deter gape-limited predators by a combination of increasing the overall body size of the prey and by making it unpalatable, or difficult, to ingest (Morgan 1987, 1989; Barnhisel 1991; Fine *et al.* 2014; see Pates & Bicknell 2019 for a fossil example) and, in extreme cases, they may even kill the predator by becoming lodged in the pharynx (Morgan 1989). This is supported by an experiment showing that grasping octopus larvae are less successful when attacking long-spined zoea compared to short-spined zoea (Nande *et al.* 2017). In some instances, spine growth can accelerate following the detection of chemical cues from predators (Hebert & Grewe 1985; Charpentier *et al.* 2017; Zhang *et al.* 2017). Despite an increased survival rate, long-spined organisms still fall prey. For instance, the long-spined zoea of the porcelain crab *Pisidia longicornis* are often found in the guts of gape-limited predators such as mackerel (Van Ginderdeuren *et al.* 2014).

Differences in the ontogenetic growth patterns of cardinal spines between *Isoxys* taxa may indicate contrasting ecological strategies. Negative allometries are documented for *I. volucris* (herein) and, to a lesser degree, *I. minor*

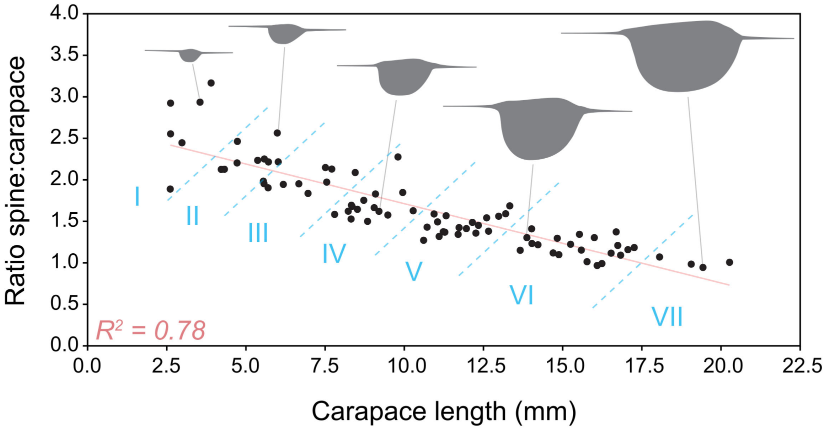

FIG. 2. Relationship between carapace length and spine/carapace ratio in *Isoxys volucris* (N = 85). Possible instar populations are indicated with numbers I–VII.

from the Qingjang biota (Ma *et al.* 2023). Positive allometries are documented for *I. auritus* from the Chengjiang biota (Fu *et al.* 2014) and *I. communis* from the Emu Bay Shale biota (García-Bellido *et al.* 2009b). Taxa in the first group primarily used their cardinal spines as a defence against predators, especially as juveniles, whereas

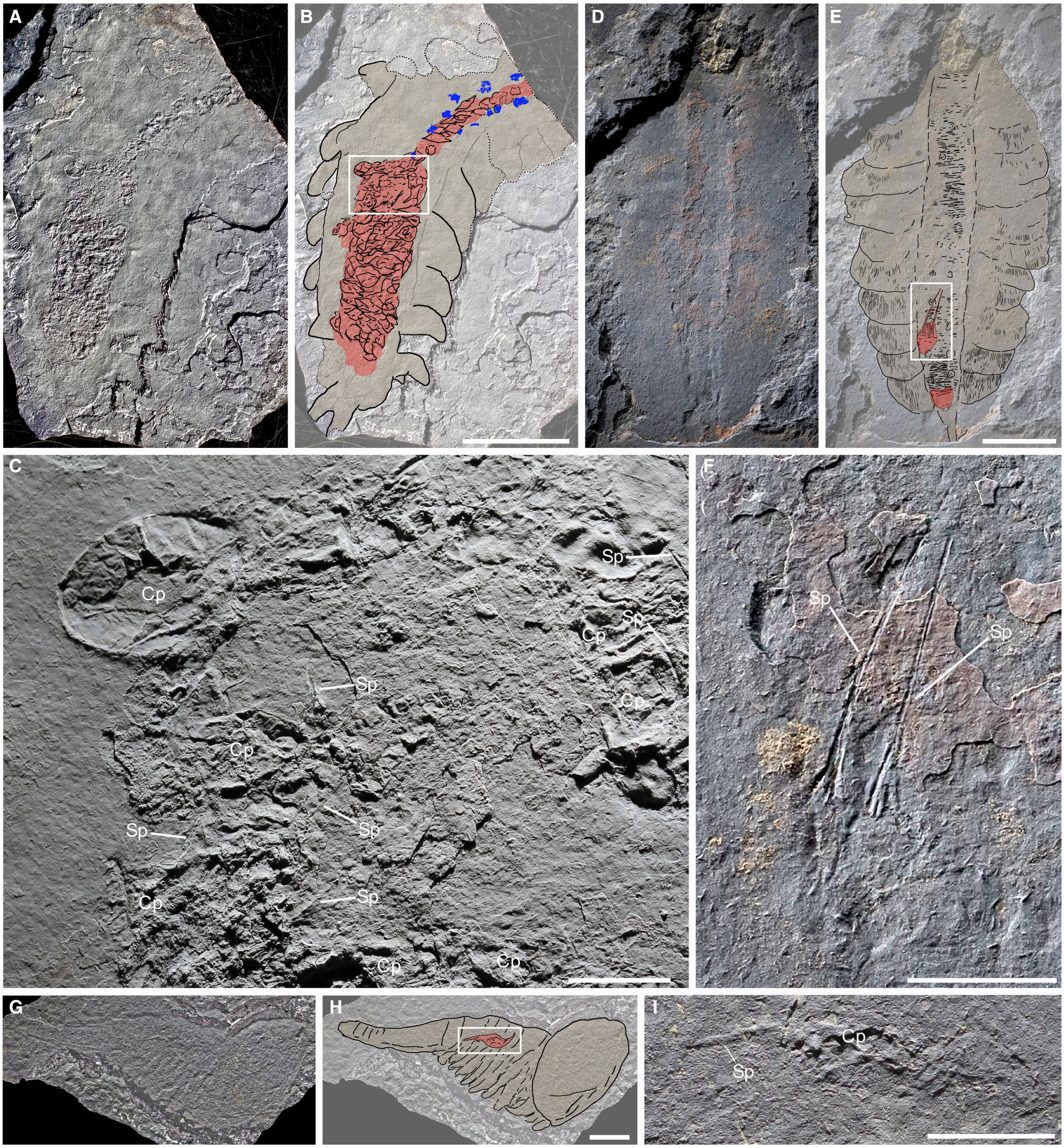

FIG. 3. Predatory taxa with *Isoxys volucris* in their digestive tract, highlighted in red in accompanying interpretative drawings. A–C, *Pambdelurion whittingtoni* MGUH 34836, digestive tract with paired diverticula (highlighted in blue) and a very high number of *I. volucris* specimens in posterior region of the digestive tract; C, closeup of digestive tract revealing *I. volucris* carapaces (Cp) and spines (Sp). D–F, *Kerygmachela kierkegaardi* MGUH 34837; F, closeup highlighting an individual *I. volucris* specimen with dislocated spines. G–I, *Pauloterminus spinodorsalis*, MGUH 34838; I, closeup of gut specimen indicating position of carapace (Cp) and spine (Sp). Images in A and G are HDR renditions, produced by integrating images taken with multiple illumination angles using Scott5 render in Photoshop. Scale bars represent: 50 mm (B); 5 mm (C, H); 10 mm (E); 3 mm (F, I).

taxa in the second group primarily used them for swimming and buoyancy. The necessity of spines to act as a deterrent in the first group evidently decreased with ontogeny, as the carapace grew sufficiently large to act as a deterrent itself. Even so, and depending on their specific morphology, cardinal spines may have had auxiliary ecological functions in both groups, as seen in modern analogues (e.g. Smith & Jensen 2015).

The exaggerated lengths of the spines in *I. volucris*, in combination with their thin needle-like shape and strongly negative allometry, suggests a particularly strong adaptational emphasis on defence compared to other *Isoxys* taxa. This implies that the taxon was under particularly high predation pressure in the Sirius Passet ecosystem. In addition to being the most abundant fossil in the fossiliferous intervals, *I. volucris* is also the most common taxon identified in the guts of predator taxa. These include the gilled lobopodians *Pambdelurion whittingtoni* (Fig. 3A–C) and *Kerygmachela kierkegaardi* (Fig. 3D–F), arthropods such as *Pauloterminus spinodorsalis* (Fig. 3G–I) and *Sidneyia*? (Peel 2017), the palaeoscolecid *Xystoscolex* (Peel 2017), and the stem-chaetognath *Timorebestia koprii* (Park *et al.* 2024). We acknowledge that there is a likely taphonomic bias in documenting prey diversity due to the unusually relief and preservation potential of *I. volucris* relative to other taxa. However, the density of *Isoxys* specimens within one specimen of *Pambdelurion* (Fig. 3A–C), amounting to 30–50 individuals, implies a particular preference for feeding on *I. volucris*.

Defensive effectiveness depends on the predator. Long cardinal spines were likely to have been more effective against gape-limited predators (e.g. large stem-chaetognaths) than against grasping predators (e.g. gilled lobopodians and arthropods). However, while the spines increased protection, they did not guarantee survival. Predators adapt counter strategies to cope with certain defensive structures. Direct evidence of the strategies of predators in the Sirius Passet Lagerstätte are inevitably scant, but one individual of *I. volucris* within the digestive tract of *Kerygmachela* (Fig. 3D–F) shows clear evidence of having had its anterior and posterior spines dislocated prior to ingestion, and of being brought into parallel alignment so that they now point towards the anterior (Fig. 3F). This is likely to have aided the passage of the prey item through the predator's digestive tract, mirroring behaviour observed amongst some living predators (e.g. preference of perch swallowing sticklebacks head-first, Hoogland *et al.* 1956).

Small, highly abundant, zooplankton-eating secondary consumers occupy fundamental lower tier trophic positions in certain modern ecosystems. For instance, krill and small pelagic fish can sustain most of the upper trophic levels in upwelling systems (Cury *et al.* 2000; Trathan & Hill 2016) and provide key links between benthic and pelagic food webs (Manno *et al.* 2020). *Isoxys* is also inferred to have fed on zooplankton (Vannier *et al.* 2009; Pates *et al.* 2021) and its sheer abundance in the Sirius Passet Lagerstätte, together with its frequent occurrence as a prey item in the digestive tracts of a diversity of middle and upper trophic level benthic and pelagic predators, suggests that it occupied a comparable fundamental trophic position in the early Cambrian food web. In this trophic position, *I. volucris* evolved a similar defensive mechanism to crustacean zooplankton in modern oceans.

CONCLUSION

Allometries of cardinal spines in *Isoxys* taxa can distinguish their primary ecological functions. The negatively allometric growth pattern of the especially long, needle-shaped cardinal spines of *I. volucris* indicate that they had a primary defensive function, to deter gape-limited predators by increasing the body size of juvenile instars. This contrasts with other *Isoxys* taxa where spine growth is positively allometric or isometric, indicating a primary hydrodynamic function.

Isoxys volucris evidences a similar adaptive response to high predation pressures as modern crustacean secondary consumers. Its common occurrence in the gut contents of several different predators in the Sirius Passet Lagerstätte, in combination with its overall high background abundance, implies it occupied a crucial trophic position in this early Cambrian ecosystem, sustaining and linking the benthic and pelagic food webs.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.70017):

Table S1. *Isoxys volucris* cardinal spine and carapace measurements.

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