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The gnathobasic spine microstructure of recent and Silurian chelicerates and the Cambrian artiopodan *Sidneyia*: Functional and evolutionary implications

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ABSTRACT

Gnathobasic spines are located on the protopodal segments of the appendages of various euarthropod taxa, notably chelicerates. Although they are used to crush shells and masticate soft food items, the microstructure of these spines are relatively poorly known in both extant and extinct forms. Here we compare the gnathobasic spine microstructures of the Silurian eurypterid *Eurypterus tetragonophthalmus* from Estonia and the Cambrian artiopodan *Sidneyia inexpectans* from Canada with those of the Recent xiphosuran chelicerate *Limulus polyphemus* to infer potential variations in functional morphology through time. The thickened fibrous exocuticle in *L. polyphemus* spine tips enables effective prey mastication and shell crushing, while also reducing pressure on nerve endings that fill the spine cavities. The spine cuticle of *E. tetragonophthalmus* has a laminate structure and lacks the fibrous layers seen in *L. polyphemus* spines, suggesting that *E. tetragonophthalmus* may not have been capable of crushing thick shells, but a durophagous habit cannot be precluded. Conversely, the cuticle of *S. inexpectans* spines has a similar fibrous microstructure to *L. polyphemus*, suggesting that *S. inexpectans* was a competent shell crusher. This conclusion is consistent with specimens showing preserved gut contents containing various shelly fragments. The shape and arrangement of the gnathobasic spines is similar for both *L. polyphemus* and *S. inexpectans*, with stouter spines in the posterior cephalothoracic or trunk appendages, respectively. This differentiation indicates that crushing occurs posteriorly, while the gnathobases on anterior appendages continue mastication and push food towards and into the mouth. The results of recent phylogenetic analyses that considered both modern and fossil euarthropod clades show that xiphosurans and eurypterids are united as crown-group euchelicerates, with *S. inexpectans* placed within more basal artiopodan clades. These relationships suggest that gnathobases with thickened fibrous exocuticle, if not homoplasious, may be plesiomorphic for chelicerates and deeper relatives within Arachnomorpha. This study shows that the gnathobasic spine microstructure best adapted for durophagy has remained remarkably constant since the Cambrian.

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1. Introduction

The four extant species of Xiphosura, commonly referred to as horseshoe crabs, are taxa familiar to both biologists and palaeontologists (Babcock et al., 2000). Biologists often use xiphosurans as model taxa to study aspects of marine chelicerates, whereas palaeontologists study horseshoe crabs largely for their extensive fossil record, spanning ca. 480 million years from the Early

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Ordovician to the Recent (Babcock et al., 2000; Racheboeuf et al., 2002; Heathoff and Norton, 2009; Rudkin and Young, 2009; Van Roy et al., 2010, 2015; Briggs et al., 2012). Furthermore, extant Xiphosura are employed as modern analogues to understand the functional morphology of extinct euarthropod taxa, such as the 508 million-year-old (mid-Cambrian) artiopodan *Sidneyia inexpectans* Walcott, 1911a from the Burgess Shale of British Columbia, Canada (Zacai et al., 2016), the early Cambrian radiodontan *Amplectobelua symbrachiata* Hou et al., 1995 from the Chengjiang biota of China (Cong et al., 2017), and a variety of large, supposedly predatorial, potentially durophagous eurypterid taxa (Selden, 1981; Babcock et al., 2000; Lamsdell, 2013; Poschmann et al., 2016).

Of the extant xiphosurans, *Limulus polyphemus* (Linnaeus, 1758) is considered here. While the biology of *L. polyphemus* is well documented, the exoskeletal cuticular microstructure is understudied. Two primary layers (in addition to the thin epicuticle) make up the chitinous cuticle of *L. polyphemus*: fibrous endocuticle that underlies a predominantly laminate exocuticle (Hock, 1940; Richards, 1949; Richter, 1969; Dalingwater, 1975; Joffe et al., 1975; Larsen, 1975; Dennell, 1978; Mutvei, 1977; Shultz, 2001; Rubin et al., 2017). No previous cuticle studies have documented the microstructural details of gnathobasic spines on the coxal segments (Fig. 1) of *L. polyphemus* cephalothoracic appendages II to VI: the features that allow *L. polyphemus* to masticate soft material and crush thin-shelled bivalved molluscs (Manton, 1964; Wyse, 1971; Wyse and Dwyer, 1973; Botton, 1984; Yamasaki et al., 1988; Botton et al., 2003). While Patten (1894, p. 90) observed that “spines on the mandibles” (presumably referring to the gnathobases) had canals and “a chitinous tubule”, no other study has sectioned the gnathobasic spines of *L. polyphemus*. The microstructure of the gnathobasic spines is therefore insufficiently documented.

We present new information on the microstructure of gnathobasic spines in *Limulus polyphemus* to determine whether the gnathobases of the Silurian eurypterid *Eurypterus tetragonophthalmus* Fischer, 1839 from Estonia, and the Cambrian artiopodan *Sidneyia inexpectans* from Canada have similar structure and function. *Eurypterus tetragonophthalmus* was chosen because of the three-dimensional preservation of appendage specimens that have been isolated from the carbonate host rock, allowing the spines to be sectioned (Holm, 1898; Selden, 1981), and the relatively close phylogenetic relationship between eurypterids and xiphosurans (e.g., Legg et al., 2013; Lamsdell, 2013, 2016; Legg, 2014; Garwood and Dunlop, 2014; Selden et al., 2015; Aria and Caron, 2017, in press). While some studies (see Dalingwater, 1975, 1987; Selden, 1981) have detailed certain cuticular microstructures of the gnathobasic spines

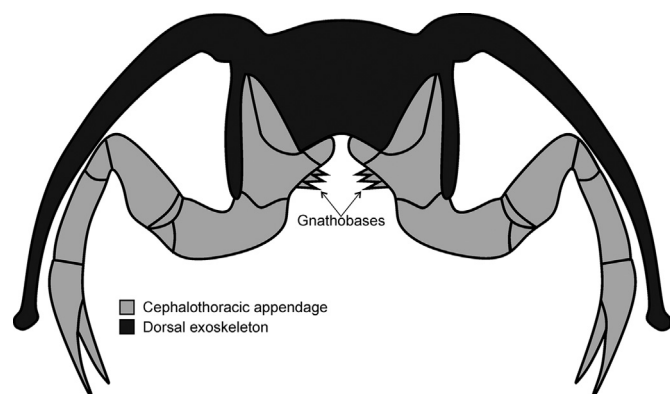


Fig. 1. Line drawing of a transverse section (in anterior view) through the cephalothorax of *Limulus polyphemus*, showing the walking legs with gnathobasic spines. The gnathobases are located on the coxa and point towards each other. Drawing modified from Selden (1981, fig. 9).

of *E. tetragonophthalmus*, no study has sectioned the spines and imaged the internal features using scanning electron microscopy. *Sidneyia inexpectans* was included as this taxon is one of the oldest gnathobase-bearing artiopodans in the fossil record, and a known durophagous predator/scavenger (Bruton, 1981; Stein, 2013; Zacai et al., 2016; Bicknell and Paterson, 2017). The exceptionally preserved carbonaceous compression fossils from the Burgess Shale (e.g., Gaines et al., 2008) have revealed some of the most intricate morphological details in Cambrian animals, including ‘cone-in-cone’ structures within lobopodian spines and claws (e.g., Caron et al., 2013, fig. 1e–k; Smith and Ortega-Hernández, 2014, fig. 1b–d). These otherwise hidden features are found using scanning electron microscope (SEM) backscatter imaging. This method is used here to show the internal microstructures of the gnathobasic spines of *S. inexpectans*.

2. Material and methods

2.1. *Limulus polyphemus*

One female *Limulus polyphemus* exuvium specimen (370 mm in length, including telson; 220 mm without the telson) housed at the University of New England (UNE; Armidale, New South Wales) was used. The fifth (right-side) cephalothoracic appendage (walking leg 4) was removed, the coxa extracted (Fig. 2A) and embedded in epoxy to make a block. The posterior side of the embedded coxa was ground down to produce a longitudinal section through the gnathobasic spines (Fig. 2B–D). Spines 2–4 were bisected, while spines 5–8 had more material removed to reveal the structural variation through the spines. The sectioned surface of the epoxy block was polished, then photographed under normal (fibre optic) lighting conditions using a Canon EOS 5D digital camera with a Canon MP-E 65 mm 1–5x macro lens. The block was later gold coated and imaged using the JEOL JSM-6010LA Scanning Electron Microscope at UNE. An accelerating voltage of 5 kV was used to acquire the secondary electron (SE) images of spine microstructures (Fig. 3).

2.2. *Eurypterus tetragonophthalmus*

One specimen of a gnathobase-bearing coxa of *Eurypterus tetragonophthalmus* (NRM Ar49987) from the Silurian (late Wenlock; Homerian) Viita Formation in Saaremaa, Estonia, was studied (Fig. 4A); the specimen is housed at the Swedish Museum of Natural History, Stockholm. This specimen was etched from the carbonate matrix using weak acids in the late 19th century and has since been dry stored (Holm, 1898). NRM Ar49987 was also embedded in an epoxy block that was ground down to produce a longitudinal section through the gnathobasic spines (Fig. 4B). Due to the disarticulated nature of the fossil, the anterior and posterior sides of the coxa relative to the body (in life position) are speculative. However, NRM Ar49987 is likely from appendage V (cf. Selden, 1981, fig. 28n). Spines 3, 4, and 6 were bisected and spines 1, 2 and 5 were not sectioned through completely to show microstructural variability (Fig. 4B). The sectioned surface of the block was polished, then imaged using the digital photographic (Fig. 4) and SEM (Fig. 5) techniques and equipment outlined in Section 2.1 above.

2.3. *Sidneyia inexpectans*

Three specimens of *Sidneyia inexpectans* gnathobasic appendages from the middle Cambrian (Series 3, Stage 5) Burgess Shale Formation of British Columbia, Canada, were studied. Specimens ROMIP 63388 (Figs. 6 and 7), ROMIP 64386 (Fig. 8) and ROMIP 64387 (Fig. 9) were collected from Walcott Quarry and are housed at the Royal

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