



Article

# Discerning the diets of sweep-feeding eurypterids: assessing the importance of prey size to survivorship across the Late Devonian mass extinction in a phylogenetic context

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**Abstract.**—Eurypterids are generally considered to comprise a mixture of active nektonic to nektobenthic predators and benthic scavenger-predators exhibiting a mode of life similar to modern horseshoe crabs. However, two groups of benthic stylonurine eurypterids, the Stylonuroidea and Mycteropoidea, independently evolved modifications to the armature of their anterior appendages that have been considered adaptations toward a sweep-feeding life habit, and it has been suggested the evolution toward sweep-feeding may have permitted stylonurines to capture smaller prey species and may have been critical for the survival of mycteropoids during the Late Devonian mass extinction. There is a linear correlation between the average spacing of feeding structures and prey sizes among extant suspension feeders. Here, we extrapolate this relationship to sweep-feeding eurypterids in order to estimate the range of prey sizes that they could capture and examine prey size in a phylogenetic context to determine what role prey size played in determining survivorship during the Late Devonian. The mycteropoid *Cyrtoctenus* was the most specialized sweep-feeder, with comblike appendage armature capable of capturing mesoplankton out of suspension, while the majority of stylonurines possess armature corresponding to a prey size range of 1.6–52 mm, suggesting they were suited for capturing small benthic macroinvertebrates such as crustaceans, mollusks, and wormlike organisms. There is no clear phylogenetic signal to prey size distribution and no evolutionary trend toward decreasing prey sizes among Stylonurina. Rather than prey size, species survivorship during the Late Devonian was likely mediated by geographic distribution and ability to capitalize on the expanding freshwater benthos.

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## Introduction

Eurypterids were a diverse and ecologically important group of aquatic chelicerates that lived from the Middle Ordovician to the late Permian (Lamsdell et al. 2015). Divided into two orders, the Eurypterina modified their most distal podomeres of their sixth appendage into paddles that they used for swimming, whereas the Stylonurina lacked this modification and used their sixth appendage for walking. Of these two clades, the Eurypterina comprise ~75% of all known eurypterid species and ~95% of all specimens, making the Stylonurina rare in comparison (Tetlie 2007). Despite their sparse fossil record, stylonurines have a longer temporal range and include the youngest known eurypterids (Ponomarenko 1985; Tetlie 2007).

While swimming eurypterids were probably active predators (Anderson et al. 2014; McCoy et al. 2015), it has been suggested the benthic stylonurine eurypterids had a mode of life similar to modern horseshoe crabs (Poschmann et al. 2016) with the exception of two clades, the Stylonuroidea and the Mycteropoidea, both of which appear to have independently evolved modifications for sweep-feeding on their anterior appendages (Lamsdell et al. 2010). Rather than hunting specific individuals, sweep-feeders capture prey en masse with strokes of their appendage armature (see “Terminology”) either through the water column as a form of active filter feeding or through the substrate as a form of rake deposit feeding. Both stylonuroids and mycteropoids possessed spines on their anterior prosomal appendages

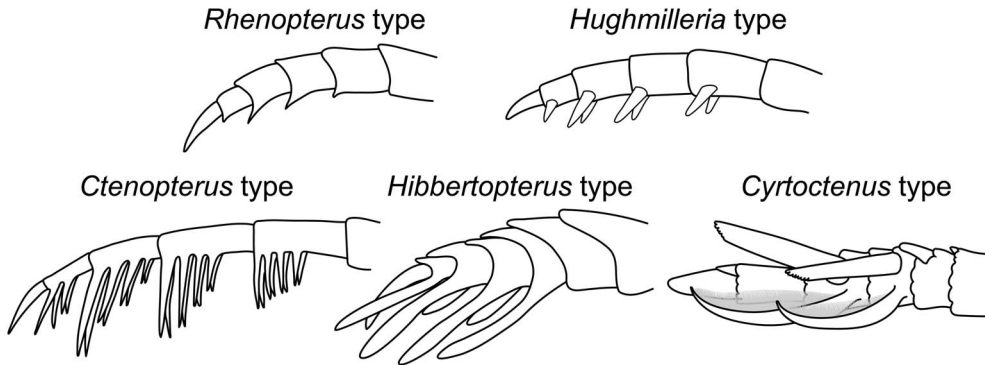


FIGURE 1. Prey-capture appendages of Stylonurina. *Rhenopterus* type appendages consist of short, fixed projections from the ventero-distal podomere margins; *Hughmilleria* type appendages possess paired movable spines at the ventero-distal podomere margins; *Ctenopterus* type appendages comprise podomeres with a series of ventrally projecting fixed spines; *Hibbertopterus* type appendages have large, broad fixed ventero-distal projections with associated broad movable spines; *Cyrtoctenus* type appendages develop large fixed filamentous rachis on the postero-lateral podomere margins with associated broad movable spines.

that they most likely used to entrap small organisms or collect food particles from suspension. Of these two clades, the mycteropoids were more specialized sweep-feeders; rather than indiscriminately raking through the surrounding medium, their armature included sensory setae which allowed them to tactilely detect organisms. While the stylonuroids did not survive the Late Devonian mass extinction, the mycteropoids radiated in the Late Devonian and persisted into the late Permian (Lamsdell et al. 2010).

The known prey-capture appendages (comprising appendage pairs II, III, and sometimes IV) in Stylonurina exhibit moderate diversity (Fig. 1), tending to be morphologically conserved in major clades. Rhenopteroidea—the clade that includes the oldest known stylonurine eurypterid, *Brachyopterus stubblefieldi* (Størmer 1951)—are characterized by the possession of *Rhenopterus* type appendages, which comprise short fixed projections on the distal podomere margins. Most clearly demonstrated in exceptionally preserved material of *Rhenopterus* (Størmer 1936), *Rhenopterus* type appendages are also recorded in the rhenopteroids *Brachyopterus*, *Brachyopterebella*, and *Kiaeropterus* (Størmer 1934, 1951). Rhenopteroids have been suggested to be bottom scavengers (Waterston 1979), a mode of life supported in at least *Rhenopterus* through studies of the visual acuity of the lateral eyes that demonstrated *Rhenopterus* to have

similar vision to modern horseshoe crabs (Poschmann et al. 2016). The anterior prosomal appendages in Kokomopteroidea, a relatively poorly known clade of Silurian–Devonian stylonurines, are only well preserved in *Kokomopterus* (Clarke and Ruedemann 1912). The prey-capture appendages of *Kokomopterus* are *Hughmilleria* type, which bear paired movable spines on each podomere, as does the sole preserved anterior appendage of the kokomopteroid *Hallipterus* (Tetlie 2008). *Hughmilleria* type appendages are also known from the stylonuroids *Parastylonurus* and *Stylonurella* (Waterston 1979). Stylonuroidea is the best known of the stylonurine clades in terms of appendage structure; as well as *Parastylonurus* and *Stylonurella*, prey-capture appendages are known from *Ctenopterus* (Clarke and Ruedemann 1912), *Soligorskopterus* (Plax et al. 2018), and *Laurieipterus* and *Pagea* (Waterston 1962). These four taxa all bear *Ctenopterus* type appendages, which consist of podomeres bearing multiple pairs of fixed spines. The close spacing and ventral orientation of the spines on the *Ctenopterus* type appendages, in combination with the greatly elongated hind-leg pairs (V and VI), led to the suggestion that these taxa may have adopted a “dagnet” style of feeding, whereby the spines were used to indiscriminately entangle soft-bodied prey (Lamsdell et al. 2010). The appendages of the final stylonurine clade, Mycteropoidea, are less well

TABLE 1. List of eurypterid specimens in which inter-armature spacing was measured. Measurements of the following specimens were derived from figures in the referenced publications: *Rhenopterus* (Størmer 1936), *Brachyoptera* (Størmer 1934), *Kiaeropterus* (Størmer 1934), *Hallipterus* (Clarke and Reudemann 1912), *C. dewalquei* (Størmer and Waterston 1968), and *C. wittebergensis* (Waterston et al. 1985). See “Institutional Abbreviations” section for specimen code prefixes.

Clade	Species	Specimens
Rhenopteroidea	<i>Brachyopterus stubblefieldi</i>	BGS D3124
	<i>Rhenopterus diensti</i>	MfN 48
	<i>Brachyoptera pentagonalis</i>	PMO H 2050
	<i>Kiaeropterus reudemanni</i>	PMO H 1711
Kokomopteroidea	<i>Kokomopterus longicaudatus</i>	FMNH UC12903
	<i>Hallipterus excelsior</i>	NMNH 25673
Parastylonuridae	<i>Parastylonurus ornatus</i>	NMS G 1897.32.69a
	<i>Stylonurella spinipes</i>	BGS GSE 87357, NMS G 1891.92.33
Stylonuridae	<i>Ctenopterus cestrotus</i>	NYSM 10276
	<i>Lauriepterus elegans</i>	NMS G1897.32.66, NMS G 1897.32.67
	<i>Pagea sturrocki</i>	NMS RSM 1956.14.11
	<i>Soligorskopterus tchepeliensis</i>	BKM 105, BKM 942
Mycteropoidea	<i>Drepanopterus abonensis</i>	BGS GSM 84701
	<i>Hibbertopterus scouleri</i>	NMS G 1987.7.10, G 55/76
	<i>Cyrtoctenus dewalquei</i>	UL RE 14786A
	<i>Cyrtoctenus peachi</i>	NMS G 1984.69.1, BGS GSE 2127
	<i>Cyrtoctenus</i> sp.	NMS G 1987.7.24
	<i>Cyrtoctenus wittebergensis</i>	USS.IT.01

known but appear to be the most morphologically diverse. The earliest mycteropoid, *Drepanopterus*, possessed appendages with fixed spines and broad movable “blades” bearing setae (Lamsdell et al. 2009; Lamsdell 2013) that may have been used as a tactile probe to detect prey (Lomax et al. 2011). The Carboniferous mycteropoids *Woodwardopterus* and *Megarachne* also appear to have possessed broad blades on their anterior appendages (Selden et al. 2005), although the available specimens do not preserve the appendages in detail. The best-known examples of appendages in Mycteropodoidea come from the Carboniferous taxa *Hibbertopterus* and *Cyrtoctenus*. *Hibbertopterus*, like *Drepanopterus*, has an appendage structure consisting of fixed spines and broad movable blades with sensory setae (Waterston 1957). *Cyrtoctenus* appears to represent an extreme modification of this appendage type, in which the fixed projections are developed into filamentous rachis that have been interpreted to function as filter devices as part of a sweep-feeding life habit (Waterston et al. 1985).

It has been shown among a diverse group of extant suspension feeders that there is a linear correlation between the average spacing of

feeding structures and prey sizes (Vinther et al. 2014). Here we extrapolate this relationship to several sweep-feeding eurypterids in order to estimate the range of prey sizes that they could capture and to compare them with other fossil and extant forms. This will offer insight into possible correlations between eurypterid prey sizes and survival rates during the Late Devonian mass extinction, when the majority of eurypterid clades became extinct. It is hypothesized that prey sizes decreased over time as sweep-feeding eurypterids evolved more complex appendage armatures and the success of the mycteropoids was due, at least in part, to their ability to capture smaller prey items.

## Materials and Methods

Measurements of inter-armature spacing were taken from specimens stored in the National Museum of Scotland in Edinburgh and the British Geological Society in Nottingham. These measurements were supplemented with those of other sweep-feeding eurypterids derived from the literature (see Table 1 for a list of eurypterid specimens included in this study).

Armature spacing results were omitted in cases where spine length did not exceed 1 mm (e.g., *Rhenopterus diensti*), as such minute armature would have been ineffective in prey capture. To assess phylogenetic trends in prey size, Spearman's rank correlation coefficient  $\rho$  (Spearman 1904) and Moran's  $I$  (Moran 1950) statistical tests were performed in R (R Core Team 2018). For Spearman's rank correlation, the distance of a species from the root of the clade was determined using the cladistic rank method (e.g., Gauthier et al. 1988; Benton and Storrs 1994).

Pectinate appendages have evolved not only in eurypterids, but also convergently at various times across several arthropod lineages, such as in numerous eumalacostracan taxa and insects (Jones et al. 2018). Furthermore, pectinate claws have evolved independently multiple times in crustaceans but differ functionally from the sweep-feeding eurypterids in that they are able to change mesh size by varying the angle at which they hold the free ramus of the claw (Tshudy and Sorhannus 2000). However, two Late Devonian fossil decapod crustaceans bore pectinate appendages in which the spines protruded ventrally in a manner similar to the Stylonurina and were included in this study for comparison. Maxilliped III of *Palaeopaleomon newberryi* and maxilliped I of *Angustidontus seriatus* were enlarged, highly spinose appendages that were capable of moving dorsoventrally (Jones et al. 2018). While *Angustidontus* is considered a pelagic predator (Rolfe and Dzik 2006), *Palaeopaleomon* possibly raked the sediment for infaunal prey (Jones et al. 2018) as has been hypothesized for several of the stylonurine eurypterids.

Inter-armature spacing for the decapods *Angustidontus* and *Palaeopaleomon* were measured from the literature. *Angustidontus* measurements were taken from specimens NMNH 530461a, NMNH 530455, and NMNH 530453a figured in Rolfe and Dzik (2006). *Palaeopaleomon* measurements were taken from specimens USNM 617308b, USNM 618374, and CMNH 4106 figured in Jones et al. (2018). The mesh sizes and estimated prey sizes of the anomalocarids *Tamisiocaris borealis* and *Pahvantia hastata* were compiled from Vinther et al. (2014) and Lerosey-Aubril and Pates (2018), respectively. The mesh and prey sizes for several modern



FIGURE 2. The benthic scavenging parastylonurid *Stylonurella spinipes* with disarticulated appendages (BGS GSE 87357). Bar indicates example measurement. Scale bar, 10 mm.

filter feeders were also gathered from the literature. Data from Jenkin (1957), Boyd et al. (1984), Budy and Haddix (2005), and Tanaka et al. (2006) compiled in Figure 4 of Vinther et al. (2014) were extracted using the WebPlotDigitizer application (Rohatgi 2018). The average mesh spacing for each fossil specimen was used to infer the range of prey sizes that could be captured by applying the lower- and upper-bound equations from Vinther et al. (2014), which are  $y = 1.4452x^{1.0083}$  and  $y = 11.772x^{0.8928}$ , respectively, where  $x$  is the average mesh spacing, and  $y$  is the estimated prey size.

Specimens were photographed with a Canon EOS 80D camera. The spacing between the distal ends of spines was measured with a caliper from photographs, with all measurements from individual specimens averaged before applying the prey size equations (see Fig. 2 for example measurement). In cases where spacing between adjacent spines varied along their lengths due to variation in the origination angle or significant spine curvature, multiple measurements were taken along the lengths of adjacent spines and averaged. Spacing measurements between adjacent spines were not taken in cases where it was not clear whether the individual spines originated from an anterior or posterior row on the appendage. Spacing measurements were also not taken between





FIGURE 3. Disarticulated sweep-feeding armature of the mycteropoid *Cyrtoctenus peachii*. A comb-rachis bearing two rows of filaments protruding from the anterior margin (BGS GSE 2127). Scale bar, 10 mm.

adjacent spines in cases where spines appeared to be missing, possibly having broken off before fossilization.

In the case of *Cyrtoctenus* armature (Fig. 3), comb filaments appeared to be flexible, with sections along the lengths of adjacent filaments often overlapping. Therefore, measurements were taken from a more proximal location along the length of the filaments, closer to where they originate from the rachis and where there appeared to be less flexion and clear separation between individual filaments. In some cases, spacing measurements could not be taken, because adjacent filaments overlapped throughout their entire lengths.

**Terminology.**—Terminology for appendage morphology follows Tollerton (1989) as modified by Lamsdell (2011). Labeling of appendages follows Selden (1981). “Armature” refers to the cuticular spines projecting from the appendages. Terminology of mycteropoid appendage armature follows Lamsdell (2013), while the movable broad spines associated with the fixed comb rachises of *Cyrtoctenus* are referred to as “fingers,” which have highly modified, dagger-shaped scales on the posterior margins termed “fulcra.” “Filaments” refers to the thin spines radiating from the comb rachis of *Cyrtoctenus*.

**Institutional Abbreviations.**—BGS, British Geological Survey, Nottingham; BKM, Trudovoy Slavy Museum, Soligorsk; CMNH, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; MfN, Museum für Naturkunde, Berlin; NMNH, Smithsonian National Museum of Natural History; NMS, National Museums of Scotland; NYSM, New York State Museum; PMO,

Paleontologisk Museum, Oslo; UL, Laboratoire de Paleontologie, University of Liege; USS, University of Stellenbosch.

## Results

The average armature spacing for most stylonurines considered to be sweep-feeders was between 1.14 mm and 4.02 mm (Fig. 4), which overlaps completely with the average armature spacing of the stylonurines not considered sweep-feeders. *Cyrtoctenus* species were outliers, with average filament spacings ranging from  $\sim 67\ \mu\text{m}$  to  $\sim 503\ \mu\text{m}$  (Fig. 5), which is more comparable to *Palaeopaleomon* ( $\sim 424\ \mu\text{m}$ ) and the pelagic predator *Angustidontus* ( $\sim 823\ \mu\text{m}$ ). There were no clear trends in prey size estimates among stylonurine eurypterids or within major clades (Fig. 6). Spearman’s rank correlation yielded a  $\rho$  of  $-0.141$ , indicating no strong directional trend in prey size within the phylogeny; therefore, armature spacing does not consistently decrease throughout stylonurine evolution. The retrieved Moran’s  $I$  value of 0.149 indicates a marginal phylogenetic clustering of armature spacing within the phylogeny, suggesting that, to some degree, closely related species have a marginally higher propensity for similar armature spacing. However, Moran’s  $I$  indicates that the distribution of appendage armature spacing is still largely random across the phylogeny.

## Discussion

**Possible Prey Items and Feeding Strategies of Stylonurina.**—The results (Fig. 4) suggest that the prey sizes that most stylonurines could capture with their appendage armatures were very similar, and thus stylonurines potentially had very similar diets. Excluding the outlying *Cyrtoctenus* values, the average armature spacing of a sweep-feeding stylonurine eurypterid was  $\sim 2.7$  mm, which provides an average prey size diameter of  $\sim 3.8$  mm to  $\sim 36$  mm. This suggests that the armature of the sweep-feeding Stylonurina was optimally suited for capturing small benthic macrofauna rather than suspended particles. Benthic macroinvertebrates such as crustaceans, mollusks, and trace fossils attributed to wormlike organisms are commonly

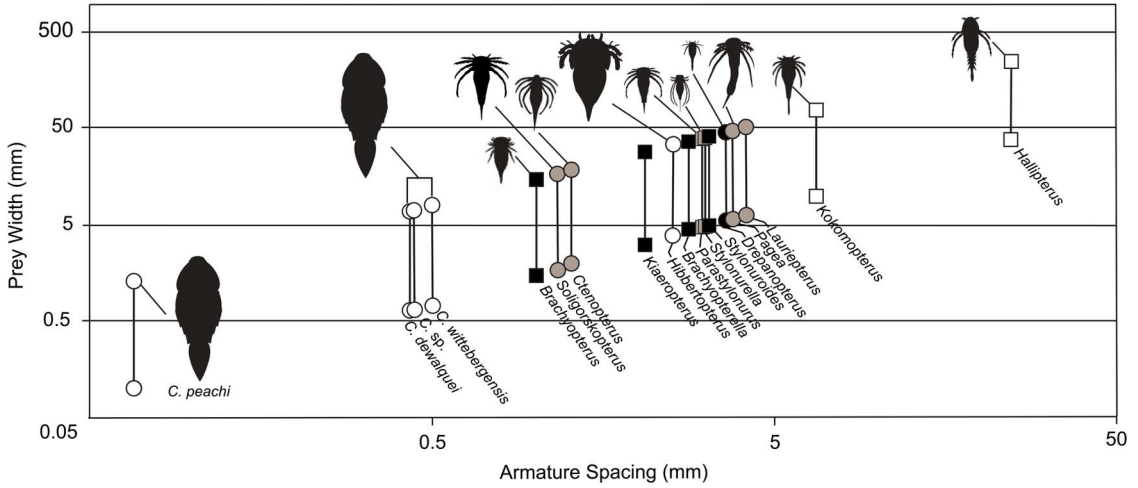


FIGURE 4. Estimated prey size ranges of eurypterids generally considered to be sweep-feeders (circles), which include stylonurids (gray), drepanopterids (black), and hibbertopterids (white), and bottom scavengers (squares), which include parastylonurids (gray), rhenopteroids (black), and kokomopteroids (white).

found in association with eurypterids and would be manageable prey items (Størmer and Waterston 1968; Clarkson et al. 1994, 2009). This is consistent with observations of modern horseshoe crabs. Adult horseshoe crabs prey primarily upon mollusks and marine worms (Botton

1984; Chatterji et al. 1992), and bivalve mollusks with shell lengths between 1 mm and 20 mm are a diet staple of *Limulus polyphemus* (Botton 1984), with bivalves >10 mm being preferred (Botton and Ropes 1989). The smaller armature spacing of *Soligorskopterus* and *Ctenopterus* suggests that

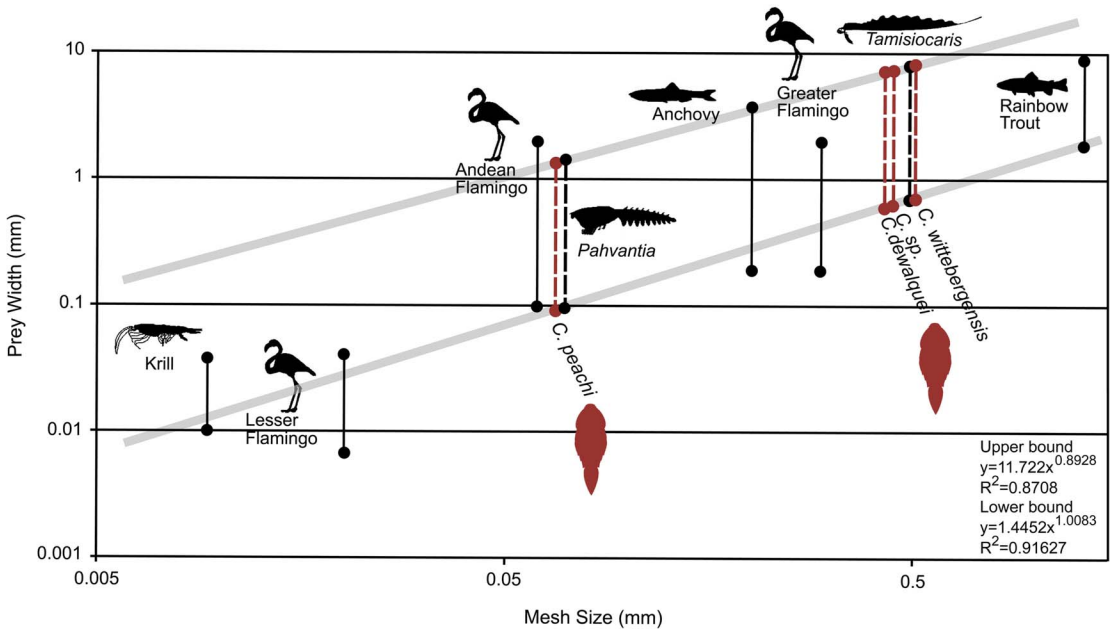


FIGURE 5. Prey size ranges of a diverse group of modern and fossil suspension feeders. Dashed lines indicate prey size ranges that were estimated from filter mesh size (modified from Vinther et al. 2014).

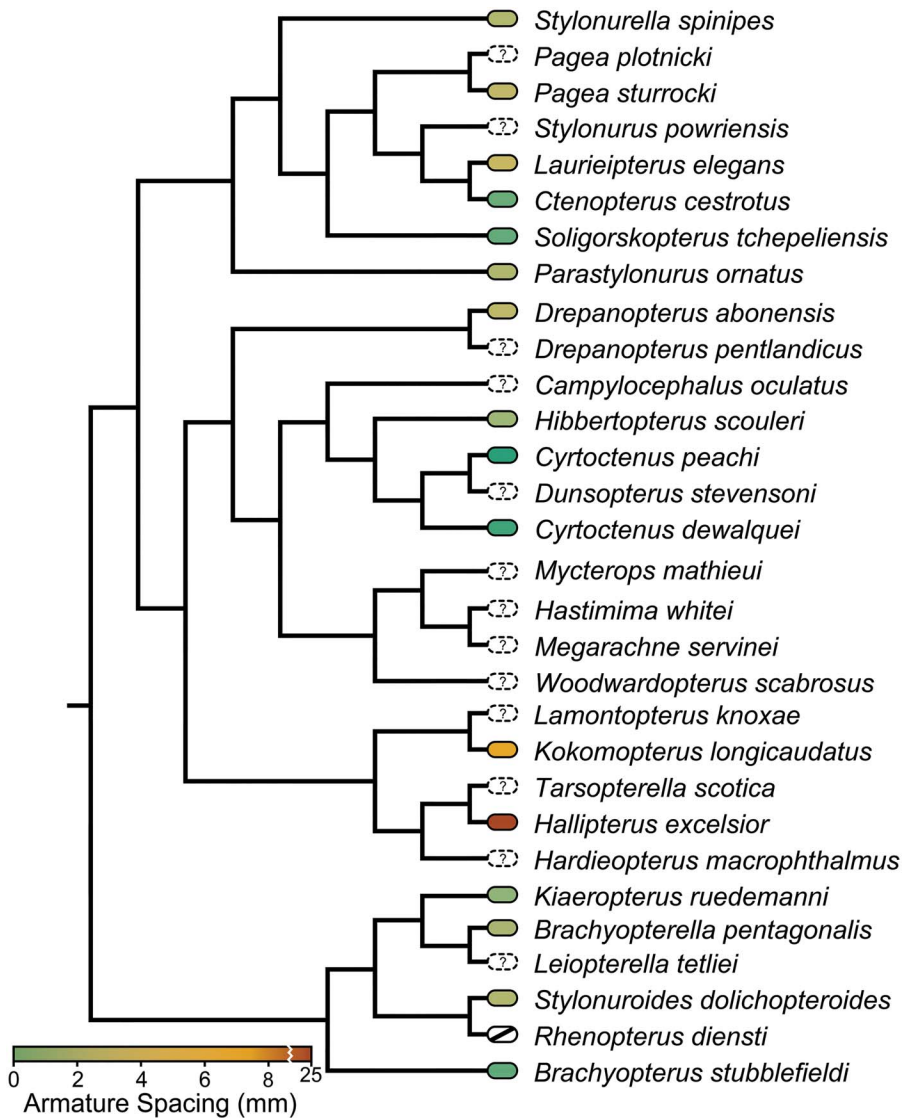


FIGURE 6. Cladogram of stylonurine eurypterids after Lamsdell and Selden (2017). Colors correspond to the average inter-armature spacing of each species.

they could also capture smaller food particles, such as benthic algae and invertebrate larvae. These prey items could have been picked directly from the appendage armature as it was drawn toward the oral region by the chelicerae. It is possible that eurypterids did not separate sediment grains from their prey; the gut content of modern horseshoe crabs includes a large proportion of sediment and microorganisms such as foraminifera, indicating that these aquatic chelicerates ingest a large amount of incidental material

with their prey (Botton 1984; Botton and Haskin 1984).

In addition to appendage armature, multiple aspects of eurypterid morphology, such as eye position, body size, and masticatory processes may provide key insights into their diets and mode of predation (Waterston 1979). The mode of life of the swimming Eurypterina contrasts with that of the Stylonurina, whose long posterior appendage pairs indicate that they were benthic crawlers or walkers. Although

several Eurypterina such as *Mixopterus* and *Megalograptus* also possessed spiniferous anterior appendages, Waterson (1979) stated that they cannot be compared functionally to the spiniferous appendages of the Stylonurina; the anterior appendages of these Eurypterina are clearly indicative of an active form of predation in which the forward-facing spines were used in active prey capture. This is in contrast to the Stylonurina, whose armature protrudes from the ventral surfaces of the podomeres, indicating food was collected beneath their prosoma. Thus, in the case of the stylonuroids and mycteropoids, it has been suggested that the anterior appendage armature was used to rake through the substrate in search of infaunal organisms (Lamsdell et al. 2009). However, if they were able to externally rotate their appendages so that their armature was directed anteriorly, they may have been capable of actively trapping prey as well.

Although morphological aspects of stylonurine eurypterids may indicate an inclination to one particular feeding strategy, they may have been generalized feeders and not specialized for just one form of prey capture or food collection. To explain the occurrence of specific trace fossils in the Devonian Campbellton Formation of New Brunswick, Canada, King et al. (2017) proposed that, in addition to active prey capture, *Pterygotus* also used its denticulate chelicerae to rake the substrate for prey (although this would have required the cheliceral claws to open to a degree that may have been functionally impossible). Additionally, modern crayfish are known to employ several feeding strategies, including active predation, foraging, and scavenging (Longshaw and Stebbing 2016). This may have also been the case with the stylonurine eurypterids. For example, *Drepanopterus* prosomal appendages retained the *Hughmilleria* type conical spines in addition to developing blades suitable for raking through the substrate. Therefore, *Drepanopterus* may have been capable of collecting smaller infaunal organisms in addition to larger invertebrates (Lamsdell et al. 2009).

The similar average armature spacings of the supposedly sweep-feeding stylonurines are comparable to the scavenging parastylonurids (Fig. 4). Thus, it may be the case that these

eurypterids were not specifically adapted to a sweep-feeding mode of life and were more generalized feeders. In addition to scavenging, they may have been capable of piercing and trapping epifaunal organisms with their appendage armatures. For example, *Pagea* may have used its long primary spines to impale organisms, while the smaller accessory spines would have prevented its victims from struggling free. The hibbertopterids, however, do appear to be specialized for sweep-feeding. The broad, blunt spines of *Hibbertopterus*, which bore sensory setae, were clearly not suitable for piercing or grasping prey, nor were the thin and flexible filaments of *Cyrtoctenus*, which were clearly adapted for straining the water for fine organic particles. However, *Cyrtoctenus* retained narrow gnathobasic teeth similar to those of *Hibbertopterus*, indicating *Cyrtoctenus* could still masticate larger food items or crush up harder shell material (Lamsdell et al. 2009).

*Cyrtoctenus* sp. (NMSG 1987.7.24), *Cyrtoctenus devalquei*, and *Cyrtoctenus wittebergensis* had nearly identical prey size estimates that range from 0.60 mm to 8.2 mm, which corresponds to a diet of mesoplankton and is very similar to the estimated prey sizes of the anomalocarid *Tamisiocaris* (Vinther et al. 2014; Fig. 5). This prey size range also overlaps with those of the greater flamingo, anchovy, and rainbow trout. The greater flamingo commonly preys upon small crustaceans such as isopods and brine shrimp (Jenkin 1957). Anchovy feed primarily on ostracods (Tanaka et al. 2006), while cladocerans are a dietary staple of rainbow trout (Budy and Haddix 2005). *Carbonita* ostracods were abundant in the Midland Valley of Scotland during the Carboniferous and fall within the estimated prey size range of *Cyrtoctenus* (Bennett et al. 2012). Filter-feeding fish such as acanthodians are often found in association with *Cyrtoctenus* and may have competed with it for similar prey items (Størmer and Waterston 1968; Evans 1999). However, *Cyrtoctenus* may have been able to avoid competition with these fish to some extent by feeding at the benthos, while acanthodians were nektonic feeders.

The estimated prey size range of *Cyrtoctenus peachi* is most comparable to that of the anomalocarid *Pahvantia* (Lerosey-Aubril and Pates



2018) and the Andean flamingo, which has a reported mesh size of  $\sim 60\ \mu\text{m}$  and a diet dominantly composed of diatoms that range in size from 0.1 mm to 2 mm (Jenkin 1957). Andean flamingos feed along the margins of lagoons and saline lakes by sweeping their bills across the surface of the substrate to suspend small food particles that can then be filtered by the lamellae within their bills as water is pumped through the oral region by the motion of the tongue (Jenkin 1957). It is noteworthy that flamingos and *Cyrtoctenus* both occupied marginal and lacustrine environments, and perhaps the appendages and movable fingers of *Cyrtoctenus* were used to disturb the substrate to suspend food particles that could then be filtered by the combs, much as Andean flamingos feed (Jenkin 1957).

*Eurypterids and the Late Devonian Mass Extinction Event.*—After enduring the Ordovician mass extinction, eurypterids radiated in the Silurian. However, decreased speciation rates in the Devonian caused diversity to decline significantly, and their lack of recovery after the Late Devonian mass extinction may have been due to their reduction in ecospace after transitioning to freshwater environments (Lamsdell and Selden 2017). Decreased origination rates in the Late Devonian have been attributed to marine transgressions that facilitated range expansions and the invasion of species that ultimately reduced instances of vicariant speciation (Abe and Lieberman 2009; Stigall 2010, 2012).

During the Late Devonian mass extinction, the Eurypterina suffered major losses, and only the Adelophthalmidae persisted into the Carboniferous (Romer 1933; Lamsdell and Braddy 2010). Abiotic factors such as marine transgressions may have reduced instances of endemism, resulting in a decline in speciation rates as background extinctions continued to reduce their diversity throughout the Devonian (Lamsdell and Selden 2017). The Stytonurina fared better, and their diversity was relatively stable throughout the Devonian (Lamsdell and Braddy 2010). During the Late Devonian and Carboniferous, mycteropoid diversity increased, and they underwent the last major eurypterid radiation (Tetlie 2007). Mycteropids and the hibbertopterids were the only Stytonurina to persist into the late Paleozoic,

and they attained a more global distribution after the formation of Pangea (Tetlie 2007). Their success has been attributed to their sweep-feeding mode of life, which would have allowed them to avoid competition with nektonic predators (Lamsdell and Braddy 2010).

It was hypothesized that as sweep-feeding eurypterids evolved more advanced armature, they would have developed finer prey capture abilities. However, there are no significant trends in prey size among stytonurine eurypterids or within major clades (Spearman's rank correlation  $\rho = -0.141$ ). Kokomopteroids had the largest average inter-armature spacing among the four major stytonurine clades (156 mm), and the basal rhenopteroids had the smallest (2.3 mm), which is most likely due to their particularly small body size. There was also no clear distinction in average armature spacing among the stytonuroids (3.1 mm for parastytonurids and 2.5 mm for stytonurids). While the mycteropoids do have a smaller average inter-armature spacing than the stytonuroids (2.1 mm and 2.7 mm, respectively), this does not hold true if the outlying *Cyrtoctenus* values are excluded (3.0 mm). Among the mycteropoids, the hibbertopterids have the smallest inter-armature spacing (1.4 mm), as was expected for these highly specialized sweep-feeders. Furthermore, armature spacing shows no preponderance to be clustered or dispersed phylogenetically, with a Moran's  $I$  value of 0.149 indicating a moderate degree of clustering but an overall distribution closer to randomness. This indicates that prey sizes are not especially phylogenetically conserved; most likely, the conflicting signal is due to the competing interactions of phylogenetic history (which would favor clustering) and ecological opportunity (which would favor dispersal) (Congreve et al. 2018). These results suggest that prey size, which neither steadily decreases over their evolutionary history nor acts as a defining characteristic of clades, does not mediate survival in the Late Devonian, and the success of the mycteropoids in comparison to the stytonuroids cannot be attributed to finer prey capture abilities.

Although eurypterids may have originally been temporarily driven to brackish and

freshwater habitats to avoid predators while they molted (Braddy 2001), chasmataspidids (Lamsdell and Briggs 2017), xiphosuran (Lamsdell 2016), and several eurypterid groups (Lamsdell and Braddy 2010) independently transitioned to freshwater environments in the Devonian, suggesting a concerted response to large, widespread environmental changes (Lamsdell et al. 2017). Their transition from marine environments may have been facilitated by the high temperatures in the Devonian, as most of the continental land masses were positioned at low latitudes (Waterston 1979). Studies of modern crabs have revealed that there is a greater tolerance to lower-salinity environments in warmer temperatures (Anger 1991). The transition to freshwater may have also been a case of ecological opportunism. In order for sweep-feeding eurypterids to have taken up permanent residence in freshwater environments, a benthic fauna must have been established in fluvial and lacustrine settings by this time. Trace fossil evidence suggests that fluvial channels and marginal lacustrine environments were first invaded by benthic invertebrates in the Devonian. During the Carboniferous, a more diverse detritus-feeding epifauna and shallow infauna became established in lacustrine environments (Fig. 7). The timing of this invasion has been attributed to the influx of nutrients into non-marine aquatic habitats from the dispersal of land plants (Buatois et al. 1998). It is noteworthy that this invasion into freshwater habitats by the benthos coincides with the radiation of the predominantly freshwater sweep-feeding mycteropoids, whose success was likely strongly contingent on the availability of such benthic prey items.

Another factor that may have contributed to the success of the mycteropoids was their geographic range. The mycteropoids were able to achieve a much larger spatial distribution than the stylonuroids, and the total range of the hibbertopterids in particular was quite extensive. *Cyrtoctenus* had the largest range among all genera; it extended from southern Gondwana to the present-day Czech Republic (Dunlop et al. 2019). Perhaps the survival of the hibbertopterids into the late Permian was partly due to their wide distribution, which

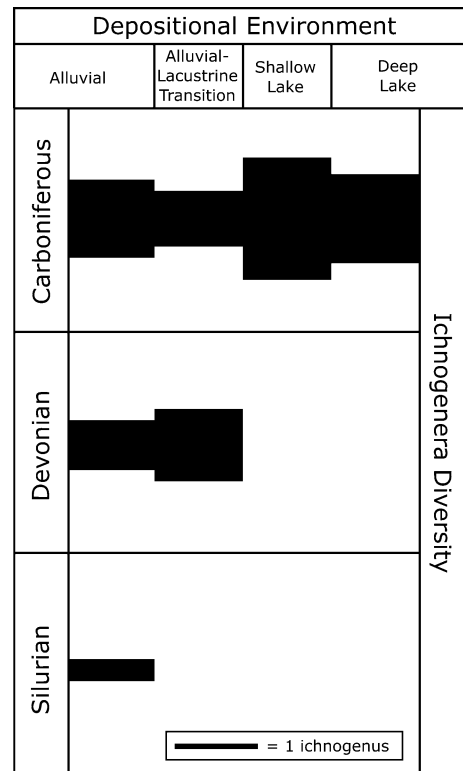


FIGURE 7. Plot of ichnogenera diversity of 166 assemblages of alluvial to deep-lake environments from the Silurian through to the Carboniferous (modified from Buatois and Mangano 1993).

would have reduced the likelihood of random events causing their extinction (Payne and Finnegan 2007; Jablonski 2008).

*Potential Sources of Error.*—Prey size estimates were based upon suspension feeders and may underestimate the true prey size of arthropods using well-developed spines for prey capture, which would have been more powerful and robust than the typical filtering structures of organisms that strain the water for food particles. Furthermore, fossil material with preserved appendage armature was limited for most taxa, and very few individuals from each species were available for inclusion in this study. Excluding the hibbertopterids, which may have developed combs capable of collecting food particles out of suspension in later molt stages, prey sizes likely increased through ontogeny as individuals achieved larger body sizes. Taking these factors into account, the estimated prey sizes likely do not

encompass the entire spectrum of prey sizes consumed by sweep-feeding eurypterids.

Because of the flexibility of the comb filaments of *Cyrtoctenus*, they likely spread outward as the appendages were swept toward the ventral body wall due to the opposing water current that was generated. Thus, their mesh sizes may have been underestimated. The dimensions of the fulcra of the associated movable fingers were measured in order to approximate the maximum inter-filament spacing. If the fulcra of the movable fingers were inserted between the filaments in order to scrape them clean and eject captured prey into the oral region, as has been suggested by Waterston et al. (1985), the fulcra may provide a reliable approximation of maximum filament spacing. The average width of these fulcra in specimens BGS 599, BGS GSE 2184, BGS GSE 2186, and BGS GSE 9682 was 0.56 mm, which provides a prey size estimate of 0.79 mm to 9 mm. Even taking into account this maximum estimate of armature spacing, *Cyrtoctenus* still has the smallest estimated prey sizes among all Stylonurina and still falls within the mesoplankton size range.

### Conclusions

The majority of eurypterids were found to have very similar appendage armature spacing, and there is no obvious distinction between those considered to be sweep-feeders and the bottom-scavenging parastylonurids, with the more closely spaced armature of rhenopteroids attributable to their smaller body sizes; while kokomopteroids had larger armature spacing as would be expected from these non-sweep-feeders. Among those eurypterids generally considered to be sweep-feeders, only *Cyrtoctenus* had an inter-armature spacing outside a range of 1.14 mm to 4.02 mm, which corresponds to a prey size range of 1.6 mm to 52 mm. This suggests that the armature of the sweep-feeding stylonuroids was optimally suited for capturing small macrofauna. Benthic macroinvertebrates such as small crustaceans, mollusks, and wormlike organisms would be manageable prey items.

The similarity of armature spacing among eurypterids with presumably different

ecological roles and the lack of more advanced modifications for sweep-feeding like those found in the hibbertopterids suggests that they may have been more generalized feeders. In addition to capturing individual benthic prey organisms, they may have been capable of trapping organisms with their spiniferous appendages. *Cyrtoctenus* was clearly a specialized sweep-feeder and has an estimated prey size range indicative of a diet of mesoplankton. This prey size range is most similar to those of filter-feeding fish like anchovy and rainbow trout, as well as flamingos.

The results of this study do not support the hypothesis that prey sizes among sweep-feeding eurypterids decreased over time, and prey size does not appear to mediate survival in the Late Devonian. While the success of the hibbertopterids may have been due to their wide distribution and sweep-feeding mode of life, which would have allowed them to avoid competition with nektonic predators, mycteropoids as a whole likely benefited from the expanding benthos, which was invading freshwater environments in the Devonian and Carboniferous.

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