

The Chelicerae of *Slimonia* (Eurypterida; Pterygotoidea)

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ABSTRACT

Pterygotid eurypterids are the most speciose eurypterid clade, accounting for almost a fifth of the approximately 250 known species, although it is unclear whether this increase in diversity is due to their increased dispersal ability, shift in predation style to cheliceral-driven prey capture, or some other factor. Determining if the development of their characteristic large chelicerae represents a key trait facilitating increased diversification is hindered by uncertainty regarding the form of the chelicerae in *Slimonia*, the sister taxon to Pterygotidae. Here I report the discovery of a specimen of *Slimonia acuminata* preserving the chelicerae in detail and corroborate reports from the 1800s suggesting that the chelicerae of *Slimonia* were short and robust. The evidence from the new specimen, taken in concert with the morphology of the rest of the animal, indicates that *Slimonia* was an active predator that captured prey with its robust prosomal appendages. The apparent increase in pterygotid species diversity therefore does indeed seem to be associated with the development of the large chelicerae; however, further work is needed to determine whether taphonomic biases in preservation due to increased sclerotization of the chelicerae or taxonomic oversplitting due to minor changes in denticle morphology are driving this phenomenon.

KEYWORDS

Chelicerate, diversity, ecology, eurypterid, feeding, Pterygotidae

Introduction

Eurypterids, also known as sea scorpions, are aquatic chelicerates that were diverse components of Paleozoic marine and freshwater communities with a geologic record extending from the Middle Ordovician (Lamsdell et al. 2015) to the late Permian (Ponomarenko 1985). Eurypterids attain an almost global distribution—with specimens recorded from every continent with the exception of Antarctica (Tetlie 2007)—and fill a variety of ecological niches ranging from epibenthic predators or scavengers (Laub, Tollerton, and Berkof 2010; Poschmann, Schoenemann, and McCoy 2016) to more active demersal predators (Anderson et al. 2014; McCoy et al. 2015) and even sweep feeders (Waterston, Oelofsen, and Oosthuizen 1985; Hughes and Lamsdell 2021). The group is known to have undergone a major ecological shift in the Devonian with multiple clades transitioning from marine to freshwater

environments (Lamsdell and Selden 2017) and at least some species of eurypterid were capable of breathing air and undertaking amphibious excursions onto land (Selden 1985; Lamsdell et al. 2020).

Eurypterids are also notable for having reached large body sizes in a number of clades (Lamsdell and Braddy 2010), with many eurypterid families including representatives more than half a meter in length (e.g., Ruebenstahl, Cieurca, and Briggs 2021). Two clades in particular, the Carboniferous freshwater sweep feeding mycteropoids (Jeram and Selden 1993; Selden, Corronca, and Hünicken 2005) and the Silurian-Devonian brackish-marine predatory pterygotids (Braddy, Poschmann, and Tetlie 2008; Briggs and Roach 2020), are famous for reaching truly giant sizes up to or in excess of 2 m. Of these two groups, it is the pterygotids that have always caught the eye of the public and researchers alike, due in part to their being by far the more commonly encountered of the

two, as well as to their predatory nature. Colloquially called “seraphim” by the Scottish quarry workers who first discovered them (Woodward 1863), the popularity of pterygotids has led to an overgeneralized perception of eurypterids as large claw-bearing predators (e.g., Laurin 2010) and suggestions within the scientific literature that competition in the form of a biological “arms race” between eurypterids and jawless vertebrates was a major driver of vertebrate evolution (Romer 1933). However, diversity shifts in the two groups are likely to be primarily influenced by major environmental and ecosystem changes that characterize the Devonian (Lamsdell and Selden 2017; Randle and Sansom 2019). Irrespective of whether or not pterygotids influenced vertebrate evolution, they were an incredibly successful group of eurypterids with an interesting evolutionary history. Pterygotids are one of the few eurypterid clades to exhibit a global distribution (Tetlie 2007), with species recorded from the paleocontinents of Baltica (Cieurca and Tetlie 2007; Naugolnykh and Shpinev 2018), Laurentia (Cieurca and Tetlie 2007; Miller 2007), Gondwana (Lamsdell, Hoşgör, and Selden 2013; Bicknell, Smith, and Poschmann 2020), and Siberia (Marshall et al. 2014), and they account for almost one fifth of the approximately 250 known eurypterid species, yet they persisted for only 46 million years, from the Llandovery (ca. 433 mya) to the Givetian (ca. 387 mya); younger pterygotids reported from South America by Kjellesvig-Waering (1964) and Olive et al. (2019) cannot with confidence be assigned to Eurypterida. In comparison, the second most diverse eurypterid family, Adelophthalmidae, also attains a global distribution but comprises just over 30 species—almost 20 less than Pterygotidae—even though the adelophthalmids span a temporal range of some 160 million years.

How pterygotids came to be so diverse is an open question. Pterygotids have a highly distinct morphology among eurypterids, with their lateral eyes being expanded and positioned marginally on the carapace; chelicerae greatly enlarged with robust denticles and an elongated proximal article; prosomal appendages II–V slender and non-spiniferous; a pretelson laterally expanded; and a broad, paddle-like telson produced into a medial carina

(Cieurca and Tetlie 2007). Numerous aspects of this unusual morphology can be linked to the adoption of an active swimming (Plotnick and Baumiller 1988) or predatory (McCoy et al. 2015) life habit; however, the morphological characteristics that define pterygotids do not develop simultaneously at the origin of the clade but instead evolve gradually among the non-pterygotid Pterygotoidea (Tetlie and Briggs 2009), comprising the genera *Hughmilleria*, *Herefordopterus*, *Salteropterus*, and *Slimonia* (Lamsdell and Selden 2017). Therefore, by studying the acquisition of characters among these taxa with reference to their phylogenetic relationships, it is possible to determine the order in which diagnostic pterygotid characteristics evolved and whether any represent key traits that contributed to the innovation and diversification of the clade (Lamsdell 2021). Of these traits, perhaps the one most conspicuously tied to predation is the enlarged chelicerae; however, the condition of the chelicera in a number of critical taxa is unknown. Although the enlarged chelicerae of the pterygotid genera *Acutiramus*, *Erettopterus*, *Jaekelopterus*, and *Pterygotus* are well known (Waterston 1964) and chelicerae of the basal pterygotoid *Hughmilleria* are confirmed to be of the shorter variety more typical of eurypterids (Clarke and Ruedemann 1912), the form of the chelicerae of the most basal known pterygotid, *Cieurcopterus*, is uncertain (Tetlie and Briggs 2009). The condition of the chelicerae in the sister taxon to Pterygotidae, *Slimonia*, is also a matter of some debate. Laurie (1893) reported that the chelicerae of *Slimonia* were short, as in other non-pterygotid eurypterids, but may have borne short denticles reminiscent of those found in pterygotids. The specimen was only figured as an unclear hand drawing, however, and the current location of the fossil itself, which had been in Laurie’s personal collection, cannot easily be traced, leading Tollerton (1989) to consider the chelicerae of *Slimonia* as unknown. Laurie’s (1893) interpretation of the chelicerae is interesting as it suggests a truly transitional morphology where denticles have begun to develop but the proximal article is not elongated, which could indicate the beginning of a shift to an active predatory life habit. However, with the only

known specimen clearly preserving the chelicerae presumed lost and the illustration of the specimen lacking adequate detail, it is necessary to find additional material to confirm the structure of the chelicerae in *Slimonia*. Here, I describe a pair of exceptionally preserved chelicerae in a specimen of *Slimonia* from the Yale Peabody Museum of Natural History collections and compare the available morphology with that reported by Laurie (1893).

Materials and Methods

All specimens of *Slimonia acuminata* are derived from the Patrick Burn Formation and the Kip Burn Formation within the Priesthill Group where it crops out in Lesmahagow, Scotland. The Patrick Burn Formation is the marginally older of the two, comprising Silurian rocks of late Llandovery to Wenlock age, whereas the Kip Burn Formation is composed of Wenlock strata (Lomax, Lamsdell, and Ciuca 2011). The eurypterids of the Priesthill Group are some of the most widely disseminated among museum collections globally, second only to the Bertie Group of New York State and Ontario, Canada, with specimens of *S. acuminata* and the co-occurring *Erettopterus bilobus* housed in numerous museums across the United Kingdom (Natural History Museum in London; National Museum of Scotland; British Geological Survey; Hunterian Museum; Doncaster Museum and Art Gallery; Oxford Museum of Natural History), Europe (Muséum National D'Histoire Naturelle, Paris; Museum für Naturkunde, Berlin), and the United States (Smithsonian National Museum of Natural History; Cincinnati History Museum; Museum of Comparative Zoology at Harvard; Yale Peabody Museum), as well as elsewhere.

The Division of Invertebrate Paleontology collections, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA (YPM IP) hold 16 specimens of *Slimonia acuminata* with limited locality information, indicating only that the fossils are from Lesmahagow. These specimens are almost certainly from the Priesthill Group, as the species has not been reported from any other geological unit and the lithology of the matrix corresponds with that of Priesthill Group specimens in other

museum collections. It is unclear whether the specimens are from the Patrick Burn Formation, Kip Burn Formation, or a mixture of the two. One of these specimens (YPM IP 033437) comprises a partially disarticulated prosoma, consisting of the dorsal prosomal shield, proximal podomeres of the prosomal appendages, and the metastoma (Figure 1).

General eurypterid terminology follows Tollerton (1989), with terminology for the prosomal structures, labeling of the prosomal appendages, and cuticular sculpture following Selden (1981). Terminology for pterygotid cheliceral morphology follows Miller (2007). Minor modifications to the terminology used in these papers follows Lamsdell (2011).

Results

The specimen (Figure 1) preserves a disarticulated prosomal carapace in dorsal view alongside the mostly articulated prosomal appendages and metastoma. The ventral prosomal structures are also observed in ventral view as indicated by the prosomal ventral plate underlying the proximal podomeres of the prosomal appendages on the right side of the specimen. The chelicerae are preserved in their entirety, while appendages II–VI are more disarticulated, preserving mostly the proximal podomeres. The ventral components of the prosoma lie along the edge of the matrix, so that the appendages on the left side and the posterior of the metastoma are not preserved. The specimen most likely represents a partially disarticulated molt, as the ventral prosomal structures are known to separate as one unit during ecdysis, with the prosomal dorsal carapace subsequently detaching from the opisthosoma (Tetlie, Brandt, and Briggs 2008).

The carapace is long rectangular in shape, 165 mm long and 95 mm wide with a length-to-width ratio of 1.73, longer than is typical for *Slimonia acuminata*, which usually has a carapace length-to-width ratio of 1.1 (Woodward 1872; Lomax, Lamsdell, and Ciuca 2011). The carapace in the Yale Peabody Museum specimen has likely been laterally compressed, as indicated by asymmetrical lateral margins and the visible wrinkles of the carapace cuticle. The lateral eyes are located in an antelateral

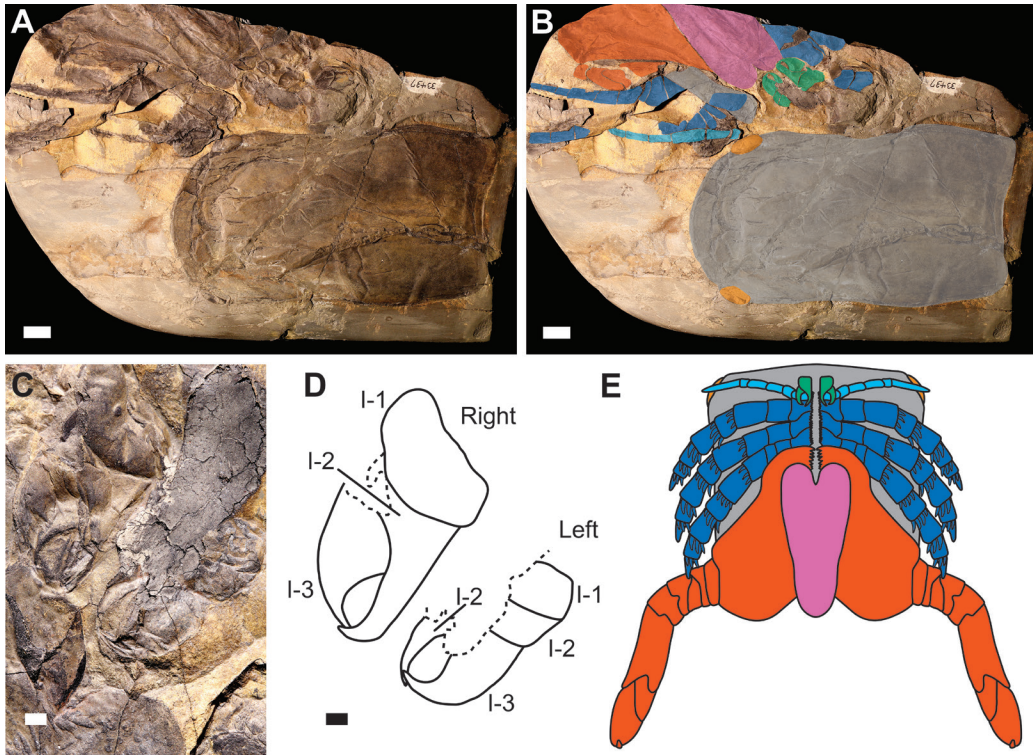


FIGURE 1. *Slimonia acuminata*, Lesmahagow, Scotland, YPM IP 033437. **A.** Partially disarticulated prosoma preserving the dorsal prosomal carapace, chelicerae, proximal podomeres of prosomal appendages II–VI, and the metastoma. **B.** With color overlay showing the various components of the prosoma. **C.** Enlarged view of the chelicerae. **D.** Interpretative drawing of the chelicerae. **E.** Reconstruction of *Slimonia acuminata* ventral prosoma colored as in B: gray for the prosomal dorsal carapace, orange for the lateral eyes, green for the chelicerae (appendage I), light blue for the palp (appendage II), dark blue for appendages III–V, red for the swimming paddles (appendage VI), and pink for the metastoma. Labels I-1, I-2, and I-3 in D denote the three articles of the chelicerae; the first article (I-1), fixed finger (I-2), and free finger (I-3). Scales bars equal 20 mm in A–B and 2 mm in C–D.

position on the carapace and are oval in shape, with a length of 17 mm and width of 7.5 mm, located overhanging the carapace lateral margin. The carapace size suggests an individual with a total length of 90 cm, which is within the range of sizes reported for the species. The elongate cardioid metastoma maximum width of 35 mm corroborates this size estimate.

The chelicerae each comprise three articles: (1) a proximal podomere, (2) a fixed finger, and (3) a moveable finger (Figure 1C and D). Both left and right chelicerae are alike in morphology and dimensions. The first article is 12 mm wide and has a length of 9 mm, although a recurved proximal margin where the podomere joins to the ventral wall of the prosoma results in the

length of the article shortening to 6 mm toward the prosomal midline as the posterior margin curves distally. The fixed finger is 15 mm long, 11 mm wide at its base and narrowing to 2 mm wide distally as the podomere extends into the finger. The finger curves into a distal hook, potentially equivalent to the terminal denticle in a pterygotid chelicera, 13 mm from the podomere proximal margin; this hook extends for 2 mm upward from the ramus of the fixed finger. The fixed finger extends along the inside (medially facing side) of the chelicera with the free finger inserting on the outside (laterally facing side) of the chelicera, as in horseshoe crabs. The free finger inserts 4 mm from the base of the fixed finger and is 11 mm long and

9 mm wide at its base, narrowing evenly to a width of 2 mm distally. The entire free finger is curved and is produced into a terminal hook (again, potentially homologous to the terminal denticle in pterygotid chelicerae) that is 2 mm wide and 2.5 mm long. The interior margin of the free finger is thickened and sclerotized, preserved as a black surface with a sharp, well-defined margin as in pterygotid chelicerae (see Lamsdell and Legg 2010; Lamsdell and Selden 2013). Aside from the terminal projections, neither finger preserves any indication of denticles.

Discussion

Comparison with Other Eurypterid Chelicerae

The observed chelicerae in the specimen described herein generally matches the description of the specimen provided by Laurie (1893), particularly with regard to the relative length of the individual cheliceral elements compared to overall body size and the curved nature of the fixed and free fingers. Whereas Laurie considered that the chelicerae of *Slimonia* may bear small denticles along their inner margins, YPM IP 033437 demonstrates the chelicerae to be devoid of denticles, with the potential exception of the curved distal terminations of the fixed and free fingers, which bear some similarity to the terminal denticles of pterygotid chelicerae.

Outside of the Pterygotidae, the form of the chelicerae is only well known for a dozen eurypterid genera, although these are well distributed across the group's phylogeny (Figure 2). Among most species the longest article of the chelicera is the second, comprising the fixed finger, which most likely represents the plesiomorphic condition given that the chelicerae of stylonurines (known from *Brachyoptera* and *Parastylonurus*) as well as those of earlier diverging clades among Eurypterina (i.e., *Moselopterus*, *Strobilopterus*, and *Eurypterus*) all fit this general morphology. The first article of the chelicera becomes proportionally longer in the sister clades Adelophthalmoidea and Pterygoidoidea, with the first and second articles being almost equal in length among adelophthalmoids (represented by *Parahughmilleria* and *Adelophthalmus*) and the pterygotoids

Hughmilleria and *Slimonia* (although in *Slimonia* the entire chelicera is short and broad). This lengthening of the first cheliceral segment culminates in Pterygotidae (represented here by *Erettopterus* and *Acutiramus*), where it is greatly elongated and extends for at least twice the length of the second article.

The relative length of the chela (defined by the length of the free finger, which inserts in the second article at the base of where it narrows into the fixed finger) also varies across the phylogeny. In the majority of taxa the free finger is less than half the length of the second cheliceral article, resulting in a relatively shorter chela; however, a number of eurypterids have chelicerae where the third article and chela is half the length of the second article. The plesiomorphic condition of relative chela length for Eurypterida is difficult to ascertain, as among the stylonurines *Parastylonurus* has a long chela while *Brachyoptera*'s chela is short; however, the consecutively short chelae of *Moselopterus*, *Strobilopterus*, and *Eurypterus* indicate that short chelae are plesiomorphic at least for Eurypterina. Two groups of eurypterines have proportionally long chelae: the Megalograptidae, represented by *Megalograptus* and *Pentecopterus*, and Pterygotidae along with their sister taxon, *Slimonia*. Both clades developed the longer chelae independently as indicated by the retention of short chelae in the pterygotoid *Hughmilleria* along with the Carcinomatidae (*Carcinosoma* and *Eusarcana*) and Adelophthalmoidea (*Adelophthalmus* and *Parahughmilleria*).

The tips of both cheliceral fingers in *Slimonia* are produced into curved projections that are likely homologous to the terminal denticles of pterygotids. The only other known eurypterid species with a hooked termination to the cheliceral fingers is *Pentecopterus*, which has a curved projection at the tip of the free finger, although this is clearly a convergent development. Neither *Slimonia* nor any other eurypterid outside Pterygotidae exhibits the development of denticles along the inner surface of the rami of the fingers. The chelicerae of *Slimonia* are also seemingly unique in the extreme curvature of the fingers, which gives the chela a more rounded cross section than in other eurypterids. The majority of pterygotid

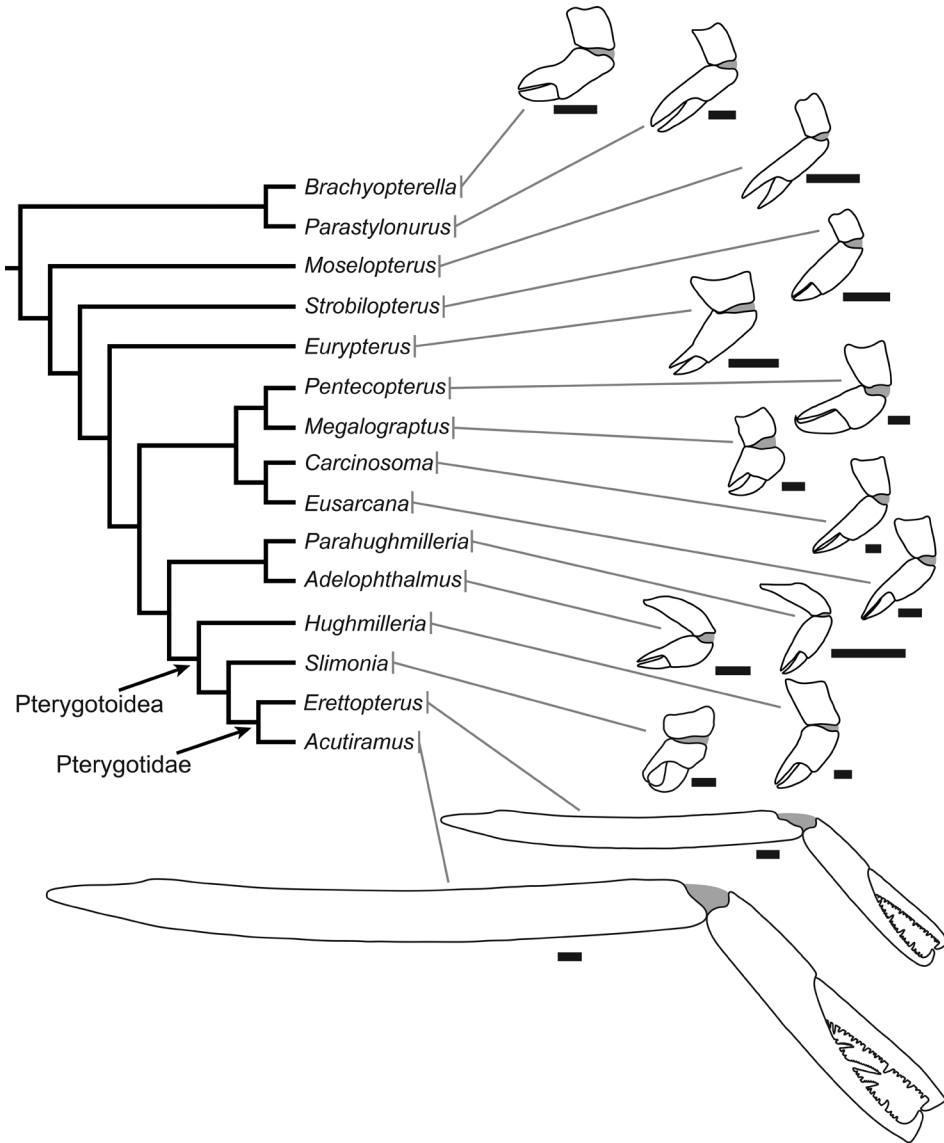


FIGURE 2. Reconstructions of eurypterid chelicerae. Each chelicera is shown in the same orientation; in lateral view with the animal facing to the right, with the attachment of the first article to the prosomal wall shown in life position. The proximal article in pterygotids is curved, resulting in the observed forward projection of the chelicera. Unsclerotized integument between the joints of the cheliceral articles is shown in gray. The relationships between taxa shown in the phylogenetic tree follows Lamsdell and Selden (2017). Sources for the morphology of eurypterid chelicerae are as follows: *Brachyopterella*–*B. pentagonalis* (Størmer 1934); *Parastylonurus*–*P. ornatus* (Waterston 1979); *Moselopterus*–*M. ancyloseton* (Størmer 1974); *Strobilopterus*–*S. princetonii* (Kjellesvig-Waering and Størmer 1952); *Eurypterus*–*E. tetragonophthalmus* (Selden 1981); *Pentecopterus*–*P. decorahensis* (Lamsdell et al. 2015); *Megalograptus*–*M. ohioensis* (Caster and Kjellesvig-Waering 1964); *Carcinosoma*–*C. punctatum* (Kjellesvig-Waering 1961); *Eusarcana* (formerly *Paracarcinosoma*; see Dunlop and Lamsdell 2012) –*E. scorpionis* (Clarke and Ruedemann 1912); *Parahughmilleria*–*P. hefteri* (Størmer 1973); *Adelophthalmus*–*A. pyrrhae* (Lamsdell et al. 2020); *Hughmilleria*–*H. socialis* (Clarke and Ruedemann 1912); *Slimonia*–*S. acuminata* (herein); *Erettopterus*–*E. bilobus* (Waterston 1964); and *Acutiramus*–*A. macrophthalmus* (Waterston 1964). Note that the chelicerae of the pterygotid genera *Jaekelopterus* and *Pterygotus* differ from *Acutiramus* only in the pattern of denticulation and so have not been included here. Scale bars equal 5 mm.

species retain the relatively straight rami characteristic of other eurypterids, although the free finger of an unnamed pterygotid from the early Devonian of China is notably curved (Wang and Gai 2014). The only other eurypterid exhibiting a curved ramus of the chelicera is *Megalograptus*, which also has a curved free finger, although not to the same degree and lacking the hooked terminal projection of *Slimonia*. The chelicerae of *Megalograptus* in fact share a general resemblance with those of *Slimonia*, both being short and robust with thick chelae, perhaps indicating a similar function or life habit for the two genera. The chelicerae of *Slimonia* therefore exhibit a mosaic of traits including pterygotoid symplesiomorphies (a relatively elongated first article), shared synapomorphies with Pterygotidae (long chela, pronounced terminal denticles on the fixed and free fingers), and autapomorphic characteristics (curvature of the free finger, squat and robust form of the chelicera). Key characteristics of pterygotid chelicerae (their large size, denticles along the finger rami, and greatly elongated first article) are therefore either synapomorphic for Pterygotidae or developed within the clade.

The Mode of Life of Slimonia

Even among as morphologically diverse a group as eurypterids, *Slimonia* is a notably unusual taxon possessing a characteristic rectangular prosomal carapace with anteriorly positioned marginal eyes, an apparently unique prosomal appendage morphology of limbs III–V, and a foliate telson. *Slimonia* is also noteworthy in its reduction of prosomal appendage II into a slender palp (Figure 1E), which likely represents the precursor to the strongly reduced palp of pterygotids (see Selden 1986), although the coxae are not fused to the labrum nor is the appendage as short as in Pterygotidae. Lomax, Lamsdell, and Ciorca (2011) considered that the reduced appendage II of *Slimonia* may have had a tactile sensory function similar to the pedipalp of spiders, and the row of pustules along the anterior carapace margin may have served as attachment points for sensory setae, with the animal searching for and identifying prey in the substrate via touch. However, *Slimonia* also possesses well-developed lateral eyes

with a high visual acuity typical of an active visual predatory lifestyle (McCoy et al. 2015), which contradicts the notion of it being a tactile benthic feeder.

Alongside the lateral eyes, a number of aspects of *Slimonia*'s morphology point to it being an active nektonic hunter of medium to large sized prey. The foliate telson is broad and has a vertically projecting dorsal keel, which, although not as well developed, is reminiscent of the laterally expanded telson and dorsal keel of pterygotids that has been shown to function in generating lift and steering while swimming (Plotnick and Baumiller 1988). The telson of *Slimonia*, as in pterygotids, is ornamented with numerous small serrations. Serrations along the telson margin are known to house attachment points for setae in other eurypterid groups (Waterston 1979), and it has been suggested that in *Slimonia* these would have allowed the animal to sense changes in water flow as it swam (Lamsdell, Marshall, and Briggs 2018). The paddles of prosomal appendage VI are also elongate and gracile with shortened, interlocking proximal podomeres and a large coxa implying the existence of very strong musculature, traits associated with an active swimming function (Plotnick 1985). While shortening of the anterior podomeres of appendages VI and lateral expansion of the distal part of the limb is a trend observed as part of early eurypterine evolution (Tetlie and Cuggy 2007), these traits are further exaggerated in *Slimonia* (Figure 1E) and can also be seen in other pterygotids, indicating increased swimming capabilities within the group. Finally, the morphology of the chelicerae in *Slimonia* suggest a gripping and tearing function. The robust nature of the chelicerae indicate that *Slimonia* may have taken relatively large prey, with the unusually broad free finger indicating a large amount of muscle within the articles, as could be expected for an organism that is restraining and rending struggling prey.

One final key to the mode of life of *Slimonia* are the structure of prosomal appendages III–V, which exhibit an apparently unique morphology among Eurypterida. These limbs are unusually large and robust—quite unlike those of most pterygotids, which are relatively delicate and without armature—and have

enlarged serrations at the podomere distal margins that are produced ventrally into thick spines. Taken in concert, the thickness of the limbs and the curved spines suggest that these limbs were heavily muscled and well suited for gripping and immobilizing prey organisms. Given that *Slimonia* was an active swimmer, it is possible that the animal adopted a mode of hunting similar to that of extant robber flies of the insect family Asilidae. Robber flies are winged predators that catch prey in flight with their robust legs and kill with a bite from their mouthparts before settling to feed (O'Neill and Seibert 1996; Ghahari et al. 2007). Robber flies are visual predators with expansive, well-developed compound eyes (Shelly 1984) and thick setal spines on the distal elements of the limbs to help hold prey in place. *Slimonia* may have had a broadly analogous hunting strategy, identifying and homing in on targets visually, capturing and subduing prey in the water column with their robust prosomal appendages, then dispatching their victim using their robust chelicerae. The density of sensory setae across the prosomal carapace margin and telson would have afforded *Slimonia* a keen sense of shifting water currents as it pursued prey, and with its lateral eyes curved around the carapace margin, it would have sight of its target even as it took hold of the prey item. Once captured, the prey could have been gripped by the chelicerae, which, with their curved morphology, share a number of characteristics with the chelifores of some pycnogonids that are adapted to piercing and holding on to prey (Dietz et al. 2018). With the robust, highly muscular nature of the chelicerae and the reinforced inner ramus of the fixed and free fingers it seems likely that *Slimonia* would have been not only able to firmly grip prey with its chelicerae but also to tear chunks off for feeding. The delicate palp of appendage II may have acted to help determine the relative position of the prey item when directly underneath the prosomal carapace but could also have had a role in manipulating and pushing items of food into the feeding apparatus formed by the coxal gnathobases of the prosomal appendages and the metastoma for mastication (Haug 2020).

Given the short morphology of the chelicerae it seems likely that, irrespective of the

exact mechanism, *Slimonia* caught and subdued prey using its robust prosomal appendages. Numerous possible prey species co-occur with *Slimonia* at the Lesmahagow localities (Rolfe 1992; Plotnick 1999): the jawless fish *Jamoytius* and *Logania*; the phyllocarid crustacean *Ceratiocaris*; the synziphosurine *Cyamocephalus*; and even other eurypterids, such as '*Hardieopterus*' *lanarkensis*, '*Nanahughmilleria*' *lanceolata*, and potentially smaller individuals of *Slimonia* and *Erettopterus*.

Potential Drivers of Pterygotid Diversity

Returning to the issue of why pterygotids are known from more species than any other eurypterid clade, it is clear that increased dispersal ability alone did not result in increased diversification. *Slimonia* also possesses the broad telson and elongated swimming paddle morphology that are considered to be the traits that permitted pterygotids to undergo transoceanic dispersal, and species of *Slimonia* are indeed known from Bolivia (Kjellesvig-Waering 1973) and China (Lamsdell pers. obs.) as well as Scotland. However, *Slimonia* does not achieve anywhere near the species diversity of any of the widespread pterygotid genera. Neither does the pterygotoid *Hughmilleria*, which is known from North America (Clarke and Ruedemann 1912) and China (Tetlie, Selden, and Ren 2007).

The proliferation of pterygotid species would therefore appear to be tied to a shift in predation habit with the development of enlarged, robust chelicerae to capture prey (Selden 1984). Interestingly *Ciurcopterus*, which is the sister taxon to all other pterygotids, is known from only two species and possesses large prosomal appendages similar in structure to those of *Slimonia*, indicating that the switch from walking limb to cheliceral-based prey capture may have occurred within Pterygotidae (Tetlie and Briggs 2009). However, while enlarged raptorial chelicerae may indeed be the reason that we find more pterygotid species in the fossil record, it may not necessarily be due to a change in ecology within the group. The pterygotid chelicera is highly sclerotized compared with the rest of the animal's cuticle, and isolated chelicerae are often the only evidence of pterygotids (or indeed eurypterids) from a given locality (e.g. Burrow, Braddy,

and Douglas 2001; Wang and Gai 2014). As pterygotid chelicerae appear to have a higher preservation potential than other aspects of eurypterid morphology, and as numerous pterygotid species are known only from individual chelicera, it is possible that the relatively high number of pterygotid species compared with other eurypterids is a taphonomic bias. It is also possible that pterygotid species are oversplit (Lamsdell and Legg 2010), with a number of species diagnosed on the basis of potentially minor or taphonomic variations in cheliceral dentition. Comprehensive restudy and analysis of pterygotid specimens will likely lead to a revision of the number of valid species and may alter our perspective of the clade's diversity.

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