Convergent Evolution Between the Mouthparts of *Eurypterus lacustris* and *Procambarus clarkii*

by

Julia Fearon

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ABSTRACT

Eurypterus lacustris has been reconstructed as a mid-sized detrivore and carnivore that was preserved in hypersaline shallow water environments (Nudds, 2008). Today, Red Swamp Crayfish (*Procambarus clarkii*) are about the same size, eat similar materials, and also live in highly variable shallow water environments (Correia, 2003). They also exhibit similar proportions in their leg segments, and have several masticating and manipulating mouthparts to aid in food processing.

I argued that this similarity in trait space may indicate convergent evolution between two distantly related groups. Gnathobasids are an ancestral trait to arthropods since the Cambrian (Bicknell, 2018), however the arrangement of longer walking legs and short feeding legs (chelicerae and maxillae) seemed to have evolved in both *Eurypterus* and *Procambarus*. I interpreted this as a convergent adaptation to eating detritus and small bottom-dwelling animals in an aquatic environment.

However, our analysis showed that *Eurypterus* and *Procambarus* mouthparts are morphologically dissimilar, and therefore do not indicate convergent evolution has occurred. I proposed that size is a large driver of mouthpart selection, and discussed new techniques such as 3D reconstruction to assess convergent evolution.

INTRODUCTION

Are eurypterid and malacostracan feeding apparatuses convergent? Eurypterids were diverse and successful chelicerates from the Ordovician to the Permian periods. They dominated in a number of different environments and ecological roles, and ranged in size from a few centimeters to two meters long (Lamsdell & Brady, 2010). Modern malacostracans, members of the sub-phylum Crustacea, embody an even greater diversity in form across many niches today. There are approximately 40,000 malacostracans, divided into 16 orders. By comparison, there are about 250 species in the order Eurypterida. However, they are closely related to the terrestrial arachnids, with 16 orders and 100,000 species. The clade Malacostraca includes a huge range of sizes and niches, including some that can be compared to the sizes and likely lines of life that were occupied in the Paleozoic by eurypterids. The two subphyla are not at all closely related, with their last common ancestor occurring in the Cambrian. Are they an example of true convergent evolution?

Convergent evolution is notoriously hard to define and quantify. Most definitions agree that convergent evolution is a process that leads to the evolution of similar forms in distantly related organisms. But how similar do traits have to be to qualify? How distantly related do the organisms have to be? There have been several attempts to quantify degrees of convergence, however, it is very difficult to quantify the similarity of form between organisms. The simplest

measure is to trace the evolution of the same form in several points in the phylogeny. I will use this method to analyze the similarity in mouthpart morphology in two very different lineages of arthropods. However, new methods often rely on Ornstein-Uhlenbeck simulations to model the probability of two lineages converging on a form. With these analyses, evolutionary biologists can measure the strength of convergence, and give greater insight into the nature of convergent evolution.

I compared the feeding apparatus of the Silurian eurypterid *Eurypterus lacustris* with that of the modern Red Swamp Crayfish (*Procambarus clarkii).* I conducted a morphological analysis of the mouth-adjacent segments in 30 *Eurypterus lacustris* fossils (Bertie Formation, New York, USA) and the maxillipeds in 32 *Procambarus clarkii* specimens to determine similarity of morphology in these two medium sized arthropods. I hypothesized that if there was convergent evolution, I would find an overlap between the principle components explaining the mouthparts.

During my research at the University of Munich, I also scanned an exceptionally preserved *Eurypterus lacustis* fossil using microCT to reconstruct the inner mouth as a 3D model. CT's ability to detect differences in density of materials allowed me to look at the structure inside the rock, not just at surface level. I used this scan to reconstruct a model of Eurypterus' leg coxae that surround the mouth. With this model, I determined the range of motion and reconstructed the movement of the mouth during mastication.

Eurypterids

Eurypterids were aquatic arthropods that arose in the Ordovician and survived until the Permo-Triassic extinction (Lamsdell & Brady, 2010). *Eurypterida* was an order that had a broad range of sizes and niches (Lamsdell & Brady, 2010). Beginning in the Ordovician period with small, marine generalists, they radiated into many different sizes and forms until their extinction at the end of the Permian. From the two-meter-long *Jaekelopterus*, to tiny specimens no more than 3 centimeters long, Eurypterida was the most diverse Paleozoic chelicerate order (Lamsdell & Brady, 2010). Informally called sea scorpions, they arose before true scorpions, and eventually inhabited fresh and brackish waters. According to tracks of Ordovician eurypterids, they may have been one of the first animals to venture on land (Braddy & Anderson, 1996; Poschmann & Braddy, 2010). In addition, eurypterids are thought to have developed book lungs or some other pathway for air breathing, although the exact mechanism has not been described (Selden, 1989). In short, they were highly successful at exploiting a variety of niches underwater, and began to colonize land.

The origins of chelicerates date back to at least the early Cambrian. *Sidneyia inexpectans* and some fuxianhuiids were considered the most basal chelicerates from the Cambrian (Yang et al. 2018). *Sidneyia* had a chelicerate-like body plan with five pairs of appendages and a mouth with gnathobasids (Bicknell, 2018b). However, it also sported a pair of antennae, which are not known in any chelicerate group. While *Sidneyia* is not considered a true chelicerate, it is similar

enough to chelicerates to constrain the chelicerate lineage at less than 518 mya (Bicknell, 2018b). This also indicates that the last common ancestor of both *Eurypterus* and *Procambarus* have been older than 518 mya.

Recent analyses of arachnids and Chelicerata (Prendini and Wheeler, 2005; Fet & Soleglad, 2005) found that scorpions were the most closely related extant taxon to eurypterids. Horseshoe crabs (*Limulus)* were also found to be a close relative.

Scorpions may be closely related to eurypterids, but they have a number of different traits, evolved to carve out a niche on land. Eurypterids and the early ancestors of scorpions both migrated out of the oceans to colonize dry land, but the scorpions have made an art of it. With a complicated system of book lungs for air breathing, sturdy legs and a stinger – a telson modified for prey capture – scorpions are well equipped for terrestrial life (Foelix, 1996). They lack swimming legs, and their walking legs are significantly bulkier to cope with lack of buoyancy on land (Dunlop & Webster, 1999). They have also adapted their eating habits to terrestrial prey. Modern scorpions are obligate carnivores, preying on insects and other small animals. They capture prey by paralyzing it with a sting, and restrain it with their claws. Then, they use their specialized mouthparts to break through the exoskeleton and suck the nutritious fluids out of the body cavity (Foelix, 1996). This is an adaptation that only works well on land, because body fluids quickly get lost in an ocean of fluid underwater. Therefore, the scorpion's mouthparts are significantly different from a eurypterid's and would not be helpful in the assessment of convergence.

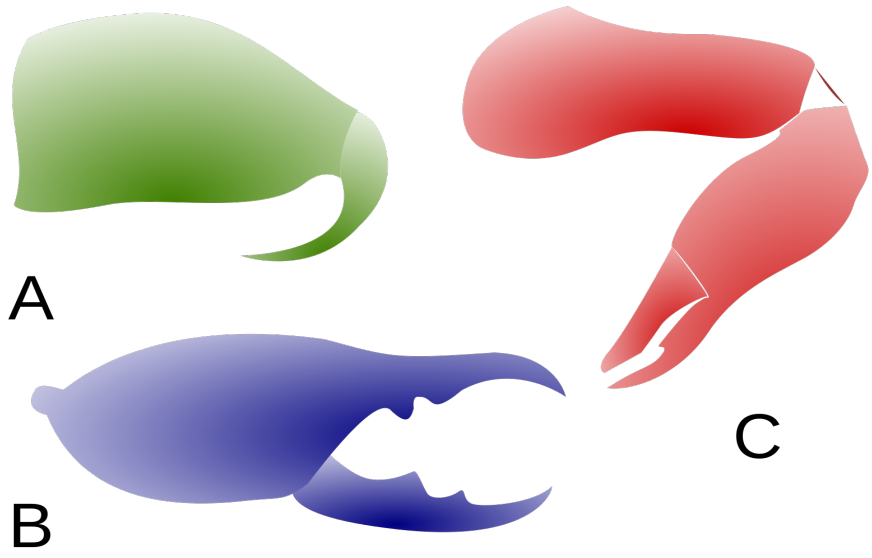

Figure 1: Chelicerae in various chelicerate groups. Chelicera A is a jackknife structure, found in *Tetrapulmonata (Arachnidae)*. Chelicera B is scissor-shaped, such as in *Solifugae (Arachnidae)*. Chelicera C is a jointed pincer, such as in *Eurypterus*. Modified from Foelix, 1996.

Eurypterida was divided in to two main groups, the *Stylonuria* and the *Eurypterina*. The *Stylonuria* as a class did not diversify as much as *Eurypterina*, but existed until the Permian extinction. This class was comparatively rarer than *Eurypterina. Eurypterina* diversified explosively in the Silurian, filling a range of niches, however all members of *Eurypterina* went extinct in the Devonian (Lamsdell & Brady, 2010).

Eurypterids possessed teardrop-shaped bodies, which supported ten legs, specialized for different uses. The first anterior appendages are the chelicerae, which are generally short grasping appendages for maneuvering food into the mouth on the underside of the head. (Tetlie, 2006). However, the chelicerae are subject to incredible diversity in length and claw size, suggesting high selective pressures on their use (Fig. 1). Analyses of chelicerae have been useful in determining diet. For example, the giant pterygotids of the Silurian are thought to have been apex predators, going after large prey such as early fish (Elliot, 2013). Placoderms from the Devonian have been found with *Jaekelopterus* chelicerae claw marks on their backs (Elliot, 2013).

The next four appendages are walking legs, useful in seafloor locomotion. Eurypterid trackways indicate that some eurypterids had the leg strength to accommodate increased pressure on land (Dunlop and Webster, 1999). There is diversity in morphology of these legs. In the Stylonuria, a group had evolved long, rake-like spines on the 2nd through 5th legs to "trawl" for prey on the seabed (Lamsdell, 2010).

Finally, the sixth pair of appendages has different morphologies in the two main groups of eurypterids. In Stylonuria, the sixth leg is also used as a walking leg. However, in Eurypterina, the last pair of legs has been modified into paddles for underwater locomotion (Vrazo & Ciurca, 2017). These large, flattened legs were thought to have allowed eurypterines, such as *Eurypterus*, to swim with a curving, up-and-down motion, reminiscent of a bird in bounding flight.

The opithosoma, the posterior half of a eurypterid's body, is composed of six preabdominal tergite segments, including one pair of Blattfüssen, followed by six more sternites, a pretelson, and a lengthened final segment, or telson, on the posterior tip. The genital appendages are located on the underside of the animal immediately posterior to the metastoma.

In the Eurypterines, the Silurian genus *Eurypterus* accounts for more than 90% of all known eurypterid specimens (Tetlie, 2007). This study focuses on *Eurypterus* specifically, because of their relatively common appearance in Silurian formations across the Northern Hemisphere. All specimens studied are either *E. lacustris or E. remipedes,* two similar species from the Bertie Waterlime Formation of western New York.

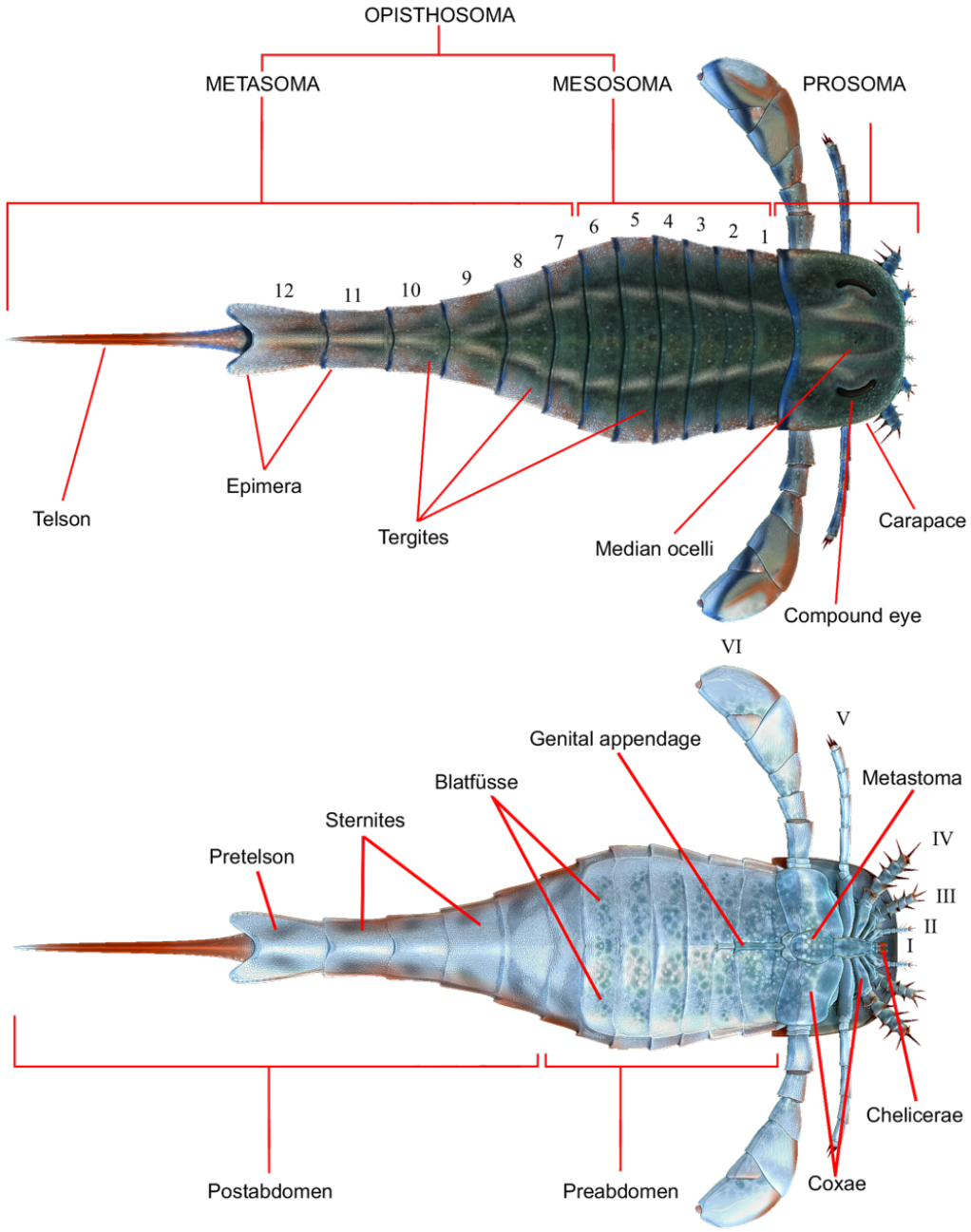

Figure 2: Labeled diagram of *Eurypterus remipedes*. Modified from art by Obsidian Soul on Wikipedia. Used under creative commons license.

Ecology and Taphonomy

The *Eurypterus* specimens used in my analysis come from one of the best known eurypterid assemblages in the world – the Bertie Waterlime. This late Silurian formation, located in northeastern New York around the Niagara Falls area east to Syracuse, is mostly made of dolomitic, thinly layered limestone, overlying shales with large gypsum and halite crystals (Vrazo, 2017). The Bertie group is approximately 17 m thick (Vrazo, 2017). Dolomite forms via the chemical replacement of the calcium ions in calcite with magnesium ions. The stoichiometric process looks like this:

$$2\ CaCO_{3(calcite)} + Mg^{2+} \leftrightarrow CaMg(CO_3)_{2(dolomite)} + Ca^{2+}$$

Rate and extent of dolomitization depends heavily on the Ca to Mg ratio in solution, surface area of the rock exposed to the ion-heavy water, high temperature, and any inhibitors that might be present (Whitaker and Xiao, 2010).

This area has been interpreted as a shallow water, closed basin environment with habitats ranging from salt flats to brackish estuary to marine lagoon. Laminations suggest that this environment experienced yearly depositional cycles (Plotnick, 1999). Desiccation cracks indicate that the formation dried out periodically. The fossils used in this study specifically come from the Fiddler's Green Formation, which exhibits multiple water depths and habitats. Lack of bioturbation and bottom anoxia in the fine carbonates is often cited as the cause of the excellent preservation (Plotnick, 1999).

This superhaline environment closely resembles modern conditions that foster penecontemporaneous dolomite formation very soon after deposition. Therefore, if dolomitization is penecontemporaneous, there is very low potential for outside deformation of the fossil (Dunn, pers. Comm.). There is always the potential for deformation through chemical replacement, but in this site there happens to be very little lost to dolomitization, and the level of detail in the fossils is quite good.

Based on modern studies of dolomitization, the area has been reconstructed as a near-shore environment that became a closed channel, trapping seawater and evaporating it into a salt pan. Other artifacts of the evaporitic environment are giant salt crystal pseudomorphs, or "hoppers", where the initial NaCl has been replaced by rock, outlining the original dimensions of the crystal. Large gypsum beds point to past salt lakes and estuaries (Vrazo, 2017).

One of the most puzzling features of this paleoenvironment is the sheer amount of *Eurypterus* fossils. Fossils are packed closely together, often resulting in two or three specimens per slab (Nudds & Selden, 2008). Heubusch (1962) proposed that all fossils found in the Bertie Waterlime were actually molts. A molt consists of a thin layer of polymerized layer of cuticle, filled with dolomite (Gupta, 2007). However, this theory has been contradicted by Vrazo (2014), as well as in this study. Vrazo suggested that *Eurypterus* might have come to this area to molt. Kjelleswig-Waering (1979) hypothesized that *Eurypterus* molts and

bodies were washed into the near-shore depositional environment from deeper waters.

Both these theories hold that eurypterids did not usually live in this environment. It does seem unusual that so many animals would have either molted or died so close together, in such an inhospitable environment. However, there is another possible explanation for the masses of fossils. Tetlie (2007) has suggested that eurypterids may have congregated to mate in this area, explaining the large number of bodies.

In addition to many eurypterid bodies and molts, the Fiddler's Green was home to large algal mats, stromatolites, nautiloids, gastropods and brachiopods such as *Whitfieldella* (Plotnick, 1999). *Cooksonia* fossils were also washed into the basin from the shore (Plotnick, 1999, Nudds & Selden, 2008). The presence of terrestrial plants in the basin indicates close proximity to the shore, as well as catastrophic water level change that could have dislodged *Cooksonia*. Unfortunately, carbonate shells do not survive dolomitization well, and most shelly fossils are known from traces and negatives (Plotnick, 1999). This community would have had to endure extreme salinity swings and differences in flow rates in brackish areas (Nudds & Selden, 2008).

In this context, Eurypterus is overwhelmingly considered a predator of smaller animals (Tetlie, 2007). To my knowledge, no formal analysis has been made of Eurypterus' mouthparts or diet, it is considered predatory because many

other eurypterids were predatory. I want to challenge this assumption in this thesis.

Malacostraca

Today, modern *Malacostraca* are even more diverse than *Eurypterida*. Crabs, lobsters, mantis shrimp, amphipods and krill are all members of this highly diverse group. They are abundant in all marine environments, and, like the eurypterids before them, have conquered freshwater and some terrestrial environments as well. Decapoda is an order of Malacostraca, and includes lobsters, shrimp and crabs. They have 20 body segments, which can each have an appendage, though most have fewer appendages (Crean, 2004). The head has antennae, mandibles and maxillae, which are associated with the inner mouth (Crean, 2004). The thorax has three types of appendages: the maxillipeds, chelipods and pereiopods. The anterior-most thorax legs are maxillipeds, which are used to delicately stuff food in their mouths (Crean, 2004; Sherman & Sherman, 1972). In crayfish, lobsters and crabs, one set of legs have been modified into chelipeds to act as a pair of claws for defense and grasping. Decapods generally use their 8 posterior pereiopod legs for walking. The abdomen can also have appendages known as pleopods (Crean, 2004; Sherman & Sherman, 1972).

I have selected Red Swamp Crayfish *(Procambarus clarkii)* as research subjects because they are common, well-known, reasonably easy to find, and

inhabit highly variable fresh and brackish water environments, which are a good analogue for the Bertie Waterlime.

Procambarus clarkii ecology

Procambarus clarkii is a devastatingly invasive species, disrupting ecosystems from East Africa to Spain. They originally hail from the Mississippi delta, and inhabit freshwater to brackish stream and lagoon environments (Alaby, 2019). They can tolerate an impressive range of water salinities and temperatures, more so than any other crayfish (Correia, 2003).

They also have an extremely broad range of prey, eating detritus consisting of plant and animal matter, as well as some live animals. Correia (2003), performed an analysis of the diets of crayfish living in Portuguese rice paddies. Crayfish in this environment tended to mainly subsist on detritus, but when small and young mostly fed on live prey. In this regard, I would consider them to have typical detritivore adaptations and behavior, which can be compared to *Eurypterus* morphology to gain insight into *Eurypterus*' diet.

Similarities in Mouthparts

Eurypterids and Decapods both have mouths on the bottom of their body cavities that have small grasping appendages. In eurypterids, there are small pointy serrations at the edge of the leg segment, or gnathobasid, towards the inside of the mouth (Bicknell, 2018a). Gnathobasids are also well-developed in one of their extant relatives, the horseshoe crab (*Limulus* spp.) (Bicknell, 2018a). However, analysis of *Eurypterus tetragonophthalmus* gnathobasids reveal they did not have the thick, fibrous coating found on Limulus gnathobasids. This indicates that this species would not be able to crack hard-shelled prey (Bicknell, 2017). In crayfish, the gnathobasic mandible is formed from the most basal segment of the appendage, and can therefore be considered roughly analogous to a eurypterid gnathobasid (Popadić, 1998). However, the structure of the gnathobasid is a bit different. *Limulus* and eurypterid gnathobasids are both curved towards the entrance to the mouth, but *Limulus* gnathobasids are much more well-developed. In crayfish, the gnathobasid is much more robust, and is covered in a hard, white substance. Part of the food processing is done by the three pairs of maxillipeds, which filter and manipulate food before it enters the mouth (Figure 3). However, after initial processing, the food enters the gastric mill, where larger pieces of food are fully pulverized.

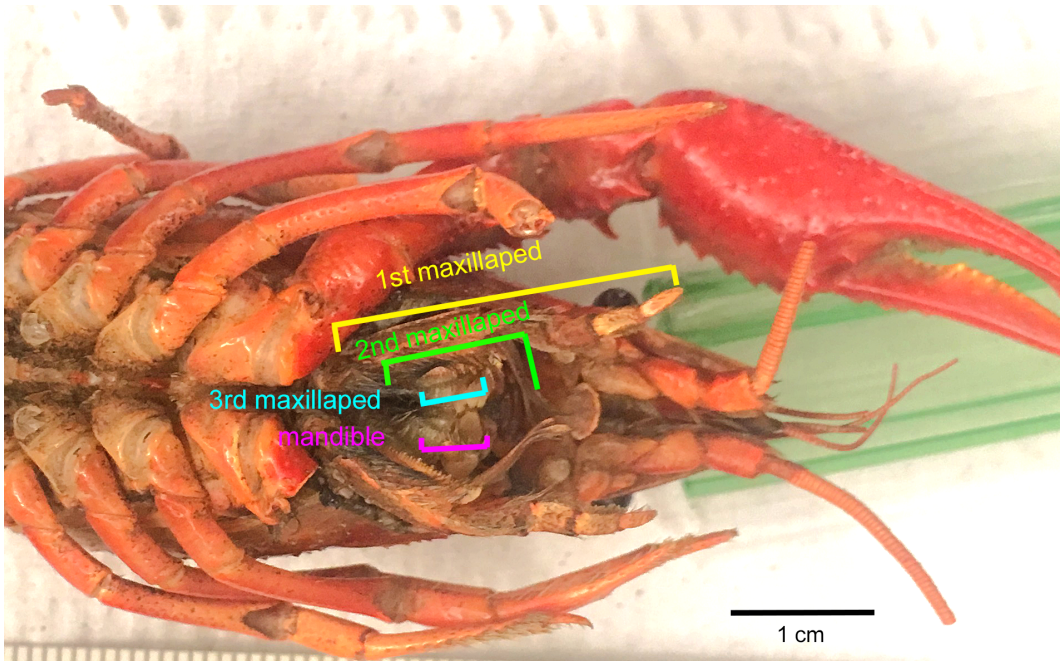

Figure 3: Diagram of *Procambarus clarkii* Mouth. The first maxilliped is outlined in yellow, second maxilliped in green, the third maxilliped in cyan, and the mandible in magenta. Scale bar is 1 cm.

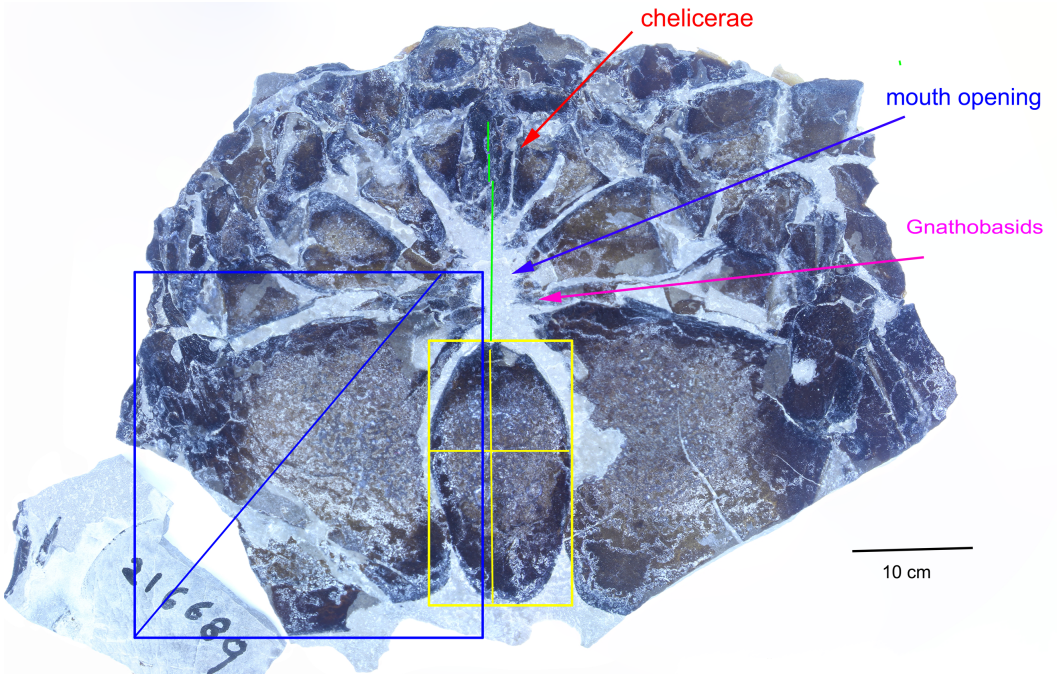

Figure 4: Diagram of *Eurypterus* mouth on ventral face of fossil. Anterior is up. Red arrow points to the chelicerae, a blue arrow points to the mouth opening in the center. A blue box surrounds the left basipodite. A pink arrow points to the gnathobasids on the basipodites. The metastoma is boxed in yellow.

Eurypterus and *Procambarus* are two of the least closely related arthropods one could name. They are separated by over 540 million years of evolution. However, their mouth shape and short appendages for food processing suggest they might be exhibiting homoplasy.

Homoplasy is the process of making similar traits that do not come from a common ancestral form of the trait. There are three ways for a lineage of organisms to create homoplasic traits: regression, parallelism and convergence. Regression, or reversion is the modification of a trait so it returns to the form of its ancestor. Parallellism is where closely related organisms develop a homoplasic trait by independently modifying an ancestral trait to both of them. The starting trait is the same, as is the ending trait, however, both organisms developed them independently. Convergence occurs when two distantly related organisms independently evolve a homoplasic trait from different starting traits.

This thesis aims to compare the mouthparts of *Eurypterus lacustris* and *Procambarus clarkii* to determine whether they demonstrate a case of convergent evolution created via similar ecological niches.

Theoretical Convergent Evolution

Convergent evolution, or convergence, in an ecological sense has been recognized for some time. Many cases of convergent evolution develop because there are a particular suite of traits that lend an advantage to certain niches in an ecosystem (Stayton, 2015). This is sometimes so prevalent that different classes of organisms will develop similar features just to eat a particular food or live in a certain environment.

The classic example is the streamlined shapes of dolphins, tuna and ichthyosaurs. All three have a streamlined shape that tapers towards a muscular tail, a dorsal fin or ridge, and two pectoral fins. However, tuna are ray-finned fish, dolphins are mammals, and ichthyosaurs are reptiles. They have all evolved a similar shape to be speedy pelagic predators (McGhee, 2011).

This type of ecological convergence is commonly found in organisms that have similar habitats, or similar food sources. In the case of these particular organisms, the mouthparts will adapt to the primary source of food, especially if the prey has adapted some kind of deterrent to predation (McGhee, 2011).

In addition to ecological convergence, there is sometimes a functional constraint of the number of forms an organism can take. Seilacher published on *Konstructionsmorphologie* (constructional morphology), which is the idea that the way an organism builds itself has physical limitations that affect the organism's morphology. He considered this on par with genetics and environment in determining an organism's final form (Seilacher, 1974). An example are the

chambers in ammonite shells. Ammonites accreted calcium carbonate to make up their shells, but only take up the front of the spiral part of the shell. They "walled up" the space behind their bodies, adding another chamber when they grew. This created the helix shaped structure with chambers, familiar to many fossil enthusiasts. Due to these limiting factors in how an organism builds a body, organisms can develop convergent traits because that trait is one of the few that are possible within the confines of its *Konstructionsmorphologie.*

There are also biomechanical constraints on how the organism can move and grow, considering its environment (Arbuckle, 2014). An organism must conform to the laws of physics in the medium in which it lives. In this way, aquatic and terrestrial animals look very different, because they have to deal with two different fluid viscosities that they live in. The second constraint is genetic. If an insect has evolved to have 6 legs, it is highly unlikely that it will suddenly be able to remodel its genome to allow for 10 legs. It is always easier to lose legs than to add them. Also, genes take up physical space on chromosomes. If a gene is located in an area with increased crossing over, it is more likely to mutate and give rise to convergent evolution. However, in paleontology, it is important not to equate genes with traits, as there is no way to obtain a genetic sequence from fossils. Third, an organism is constrained by its environment and ecological niche. Organisms interact with prey, predators and non-living objects on a day-to-day basis. Certain niches have adaptations that work well for those roles, and organisms that inhabit that niche, may take on that trait.

Measuring Convergent Evolution

Convergent evolution has not been studied as thoroughly by evolutionary biologists as other forms of evolution, because it is difficult to diagnose and model (Stayton, 2015). It is very easy to observe that two organisms look similar but it is extremely difficult to quantify that similarity. In science, Justice Potter Stewart's famous line, "I know it when I see it", is hardly acceptable. Thus, proxies for similarity of form are commonly used to quantify convergent evolution.

Evolution is any change in the hereditary genetic makeup of a group of organisms over time. Any change in the frequency of a particular allele in a population, even by chance, is considered evolution. Groups of organisms, from a population to a species, are not static entities. They are constantly changing in genetic makeup even if no selection is occurring. Organisms may randomly die or be unexpectedly successful, thereby under- or over-representing their genes in the group. This "evolution by chance" is called genetic drift.

However, if genetic drift is happening all the time, how is it possible to tell if selective evolution (such as natural selection or convergent evolution) is actually happening? Wouldn't selection get lost in the noise of genetic drift?

To counteract this problem, evolutionary biologists assume a baseline of genetic drift. A popular baseline over the past ten years has been dictated by Brownian Motion, the mathematical description for random motion of particles suspended in a fluid (Arbuckle, 2014; Stayton, 2015). Brownian Motion is

completely random, and so gives a good baseline for genetic drift. It can also approximate a genetic drift-mutation balance, and model stabilizing selection (Stayton, 2015). However, simple Brownian motion cannot explain all instances of evolution.

Ornstein-Uhlenbeck modelling is an expansion of the Brownian motion model that allows for selection towards a morphological "goal" or optimum trait value. Hansen (1997) modelled this process with one optimum trait value. However, this assumes that all groups at a particular branch of the phylogenetic tree measured within that model are headed towards the same optimum trait value.

Butler and King (2004) assumed that several distinct selective regimes were acting on a quantitative trait, and gave each branch a small number of potential optimum trait values. Furthermore, Beaulieu et al. (2012) created a model where the strength of selection towards the optimum trait value, and the total stochastic evolution, were not confined to a constant rate, but could vary.

However, Ornstein-Uhlenbeck modelling has its limitations. For one, it assumes few optimum trait values, and assumes the same rate, or rate of change, for all groups involved (Arbuckle, 2014). It does not work well with small datasets (Cooper, 2016). It also relies on either trait scoring or using molecular data. Molecular data cannot be collected for a fossil. Therefore, it is not useful in this study.

Regression

I suggest that regression (also called reversion) is not a factor, because eurypterids are extremely distant from crustaceans on the evolutionary tree. Regression is a similarity to a previous ancestor. However, *Eurypterus* and *Procambarus* are so distantly related, that their closest common ancestor is nothing like either of them. Eurypterids and crustaceans diverged at the subphylum level, as crown-group arthropods, in the Ediacaran (Figure 5). The oldest presumed chelicerate is a Cambrian arthropod, *Sidneyia inexpectans*. *Sidneyia* differs from later chelicerates because it has a pair of antennae. Otherwise, it is similar to other chelicerates in body organization and presence of chelicerae. *Sidneyia* is a paddle-shaped arthropod with spiny gnathobasids. This mouth plan with the spiny gnathobasids is ancestral to prior to Xiphosura (Bicknell, 2017). Bicknell's analysis of *Sidneyia*'s gnathobasids compares them to modern horseshoe crabs *(Limulus*) and eurypterids. Its gnathobasids originate from the fifth basipod and are considered an ancestral trait to chelicerates. Gnathobasids on other coxae are basal to all true arthropods (Popadić, 1996). Their microstructure was interpreted by Bicknell et al. as a specialized mechanism for crushing shells. The fibrous exocuticle in *Limulus* is strong enough to crack open a clam. His analysis of the microstructure determined that while *Sidneyia* could likely crack hard-shelled prey, *Eurypterus* would not have had thick enough cuticle on the gnathobasids, nor the right leverage to crack shells.

In this thesis, I will look at convergent evolution between two genera of organisms: *Eurypterus* and *Procambarus*. I will also investigate *Limulus,* one of the eurypterids' closest living relatives, to see what is due to ancestral similarity, and what is a novel synapomorphy that may indicate convergent evolution.

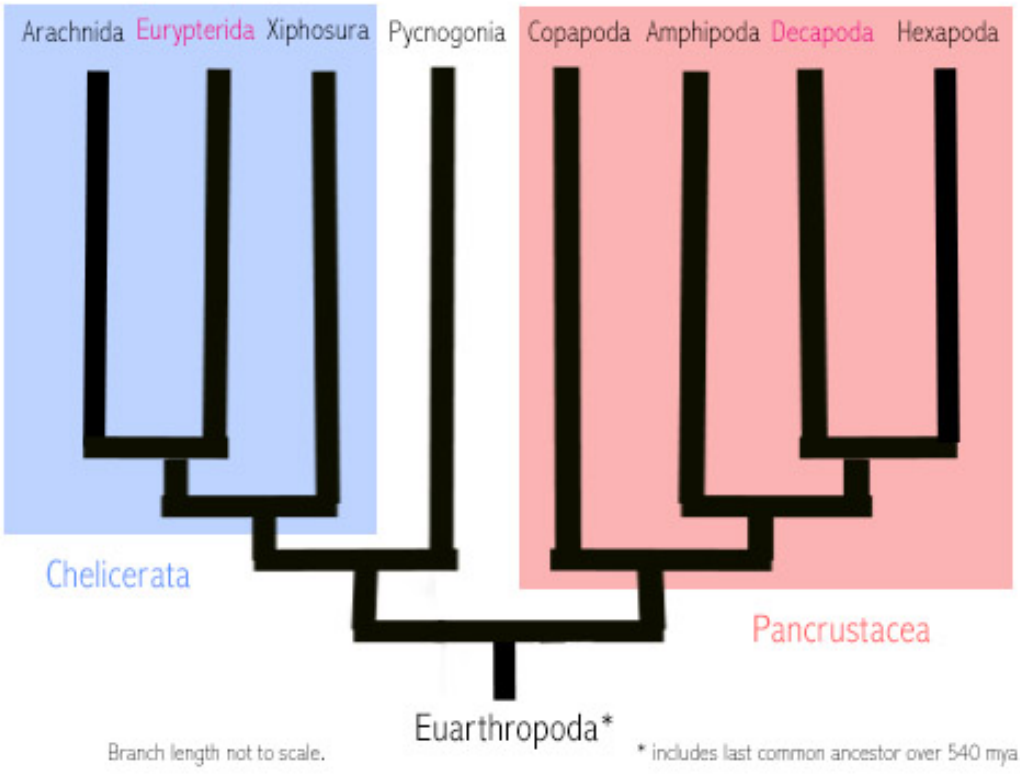

Figure 5: Simplified cladogram of Euarthropoda, showing the lineage of Eurypterida and Decapoda. The common ancestor of both is shown at the bottom of the cladogram, and would have appeared before 540 mya. Chelicerata is indicated with a blue box, while Pancrustacea is indicated with a red box. Groups of interest (Eurypterida and Decapoda) are highlighted in pink. Branch lengths are not to scale, and do not correspond with events in geologic time.

METHODS

As mentioned before, there are many difficulties in quantifying convergent evolution. For one, there is difficulty in discerning the convergent trait itself, defining how similar the traits must be, and investigating the paths that lead both organisms to their homoplasic trait.

In this chapter, I will explain why I chose these particular organisms, delineate the exact structures I am comparing between *E. lacustris* and *P. clarkii*, and present my process for their measurement and comparison. I will also describe the process of making a 3D model of a *Eurypterus* forebody, and the manipulations required to reconstruct the dimensions of the original creature before taphonomy. I will also explain how 3D modelling can be used as an aid to biomechanical analysis.

Measurements

I measured 32 *Eurypterus* fossils, 30 *Procambarus* specimens, as well as 7 dried *Limulus* specimens to determine the average dimensions of these organisms' ventral body segments. Multiple measurements were made from each specimen. Unfortunately, even with exceptionally preserved specimens, many of the fossils did not exhibit all the body parts I planned to measure, so several specimens had to be left out of the final analysis. For example, not all of the fossils included the *Eurypterus*' opisthoma, so I could not obtain a length of body from anterior tip to

telson. This left me with 21 usable *Eurypterus* fossils and their corresponding measurements.

In preparing measurements, first, I had to determine *what* to measure. I wanted to measure the mouth, as well as the chelicerae/maxillipeds. However, in many eurypterid fossils, if the ventral side of the animal is preserved at all, it is often deformed during or after deposition. The negative space where the mouth used to be is rarely the size it would have been in life – often a coxa will have encroached upon, or even completely covered the mouth. So, to record the negative space of the mouth, I measured the length and width of the coxae surrounding the mouth. I also measured the diagonal of the basipodites, the coxa of the 5th leg, or swimming leg. I also measured the length, width, and length of the notch in the metastoma, a seqment in the forebody located in between the two basipodites (Fig. 5). The metastoma is unique to eurypterids, so I was not able to compare analogous structures in crayfish. Measuring the maxillae and chelicerae was comparatively straightforward. I only measured the length of the chelicerae of the *Eurypterus* specimens, and measured 1st, 2nd, and third maxillapeds in the crayfish.

I also measured 30 crayfish (*Procambarus clarkii*) to compare to the eurypterid data in that morphospace. I had considered using lobsters, but they would be expensive to obtain and not have a size distribution needed to make a good comparison to *Eurypterus lacustris*.

I wanted to have reproducible measurements, so I took high-resolution photos of all specimens, drew measurement axis lines on the image, and measured the images digitally. The crayfish were measured with calipers, but I also took photos and re-measured digitally to check the data and to keep the method consistent.

Eurypterid Measurements

Photos were taken with a Canon EOS 700D. Images were stacked using CombineZP, and then stitched together using Photoshop 13 Elements and Adobe Photoshop CS3. Some detail shots were made with a VHX-6000 Photomicroscope.

Measurements were made using Adobe Illustrator, Photoshop 13 elements and ImageJ/Fiji. Images with axes used for measurement are available.

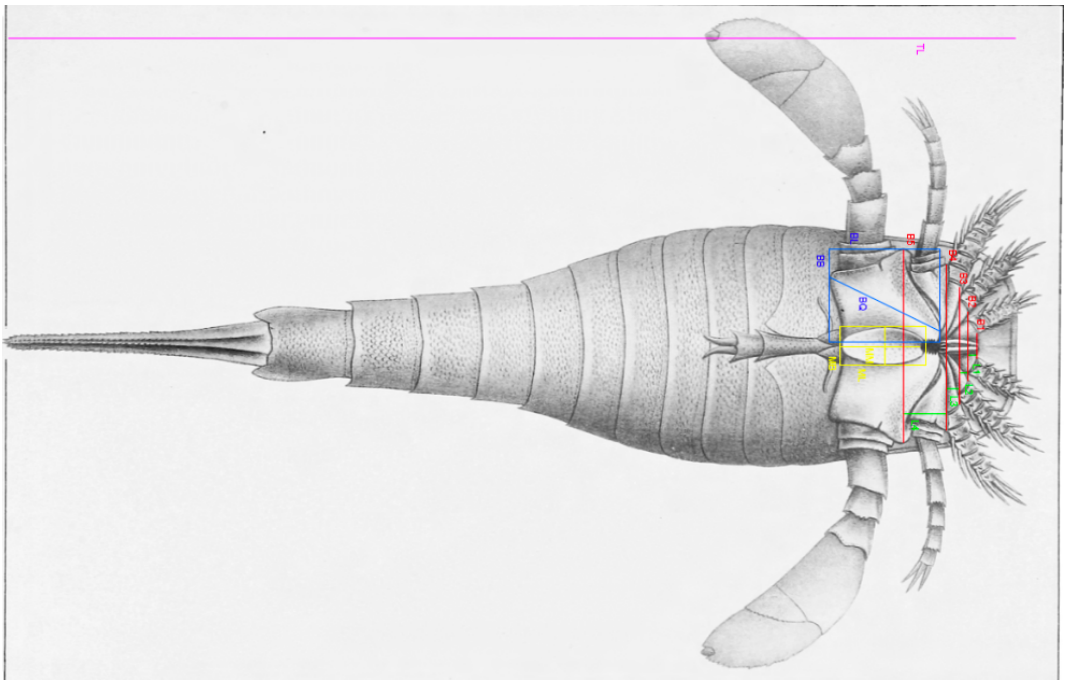

Figure 6: Eurypterid measurement schema on the ventral side of a *Eurypterus* illustration. Colored lines correspond with measurements recorded. Total length is visualized in pink, width of coxae is visualized in red, and length between coxae are visualized in green. Length, width and diagonal of the basipodites are in blue, and length and width of the metastoma are in yellow.

Crayfish Measurements

I measured 22 crayfish (Whole Foods, Bayou Pigeon, LA), and noted length and spacing between the base of the walking legs, total length, maxilliped lengths, mandible length, weight, and distal width of the large claw.

Crayfish were defrosted at room temperature (20*C) for about 45 minutes until tail was fully pliable. Specimens were weighed on a Brainweigh B200 scale. Crayfish were then measured using calipers according to the aforementioned diagnostics. To accurately measure the maxillipeds and mandible length, maxillae and mandibles were removed surgically and then measured. Once maxillae had been removed, the full specimen was photographed with a smartphone camera for further digital measuring through imageJ. Specimens remeasured in this way were examined in a similar manner to the eurypterid measurements described above.

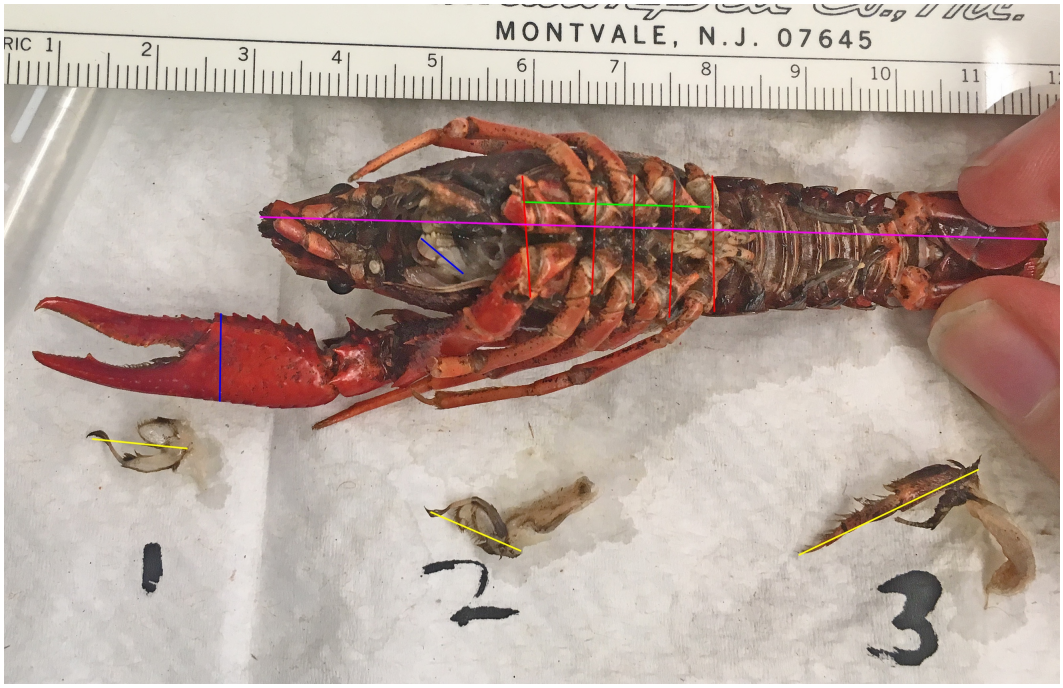

Figure 7: *Procambarus* measurement schema on the ventral side of a specimen. Colored lines correspond with measurements recorded. Total length is visualized in pink, width of coxae are visualized in red, and length between coxae are visualized in green. Width of the claws are in blue, and length of the three maxillipeds (dissected out and labeled at the bottom of the figure) are visualized in yellow.

Limulus Measurements

Dried *Limulus polyphemus* specimens were measured manually with calipers. I attempted to make measurements of analogous segments to Eurypterids, that is: length of chelicerae, length and width of the first through fifth coxae surrounding the mouth, and the diagonal of the basipodite. As *Limulus* do not have metastoma, metastoma measurements could not be described. Weight could not be described.

Statistics

I performed a principal components analysis in R using the vegan package and the ggbiplot package (Dixon, 2003; Yan, 2000). My qualifications for convergence were overlap in the principle component scores of the most clustered 90% of the *Eurypterus* and *Procambarus* data. This was visualized with a graph of the principle component scores with an oval drawn around each species group, encompassing 90% of that species' data. If the ovals overlapped, then the principle component scores overlapped.

3D modelling

I also created a 3D model of a eurypterid forebody. I MicroCT scanned fossil YPM-364 (*Eurypterus lacustris*) at the Zoologischesstaatsmuseum Bayern, or Zoological State Collection of Bavaria (ZSM). At first, the model was

processed in Microscope Image Browser (MIB), however, the interpolation was grainy, so I attempted again in OsiriX. The model was processed much better in OsiriX, and visualized and refined in Blender. To cope with the large size of the original CT scan, I resized the original file.

The difference in density between the fossil and the matrix was not dramatic, so fossil delineation had to be done manually. With the file, I created ROIs in OsiriX by drawing around the boundaries of each fossilized segment by hand. I cut the model around ROIs, and made .obj files. Then, I ported .obj s into Blender to render the model. I applied Decimate filter down to 0.1 to smooth the model, and Applied the Subsurf filter to improve the texture. I also colored it to make leg identification easy.

To create the 3D printed model, I converted the model into .objs and used Meshmixer to fix many of the “holes” in the model. Then, I was able to print using the Ultimaker gear printer in the Fimble Maker and Innovation Lab at Mount Holyoke.

Live Animal Analysis

Two live *Procambarus* were handled and measured. One male and one female were measured. Specimens were photographed and measured from photos in the same manner as the fossils. Crayfish were fed small bloodworms to better inspect their eating process. Video footage of feeding was taken to better isolate the structures involved in the feeding process.

One live *Limulus* was handled from November to December. This specimen was also measured from photos via ImageJ. The *Limulus* was placed in a 10-gallon tank for observation, and fed bloodworms. The *Limulus* was observed from below to observe the feeding process. Video recordings were made from below and at substrate level to observe the anterior end of the animal.

RESULTS

Principal Component Analysis

Principal component analysis is a method to determine factors that vary together and may explain variability seen in the data. Components are made of any number of factors that happen to vary together (for example: size, age, leg length, ect.) The principal component analysis found a high adherence to our first and second components. The first variable explained 0.776 of the variance in the data, and the second variable explained .193 of the variance in the data. The rest of the variables explained less than 2% of the data.

However, when graphed, the *Procambarus* and *Eurypterus* data did not overlap at all (Fig. 7). *Procambarus* data mostly remained tightly clustered around about 0 on the first component, and -1 on the second component. The *Eurypterus* data had a bigger range on the first component axis (from -3 to 2), but had much higher component two scores (from 0 to 2). Eurypterus data had more spread, while the *Procambarus* data was very precise and tightly clustered. I attributed this to the standardization of commercial crayfish.

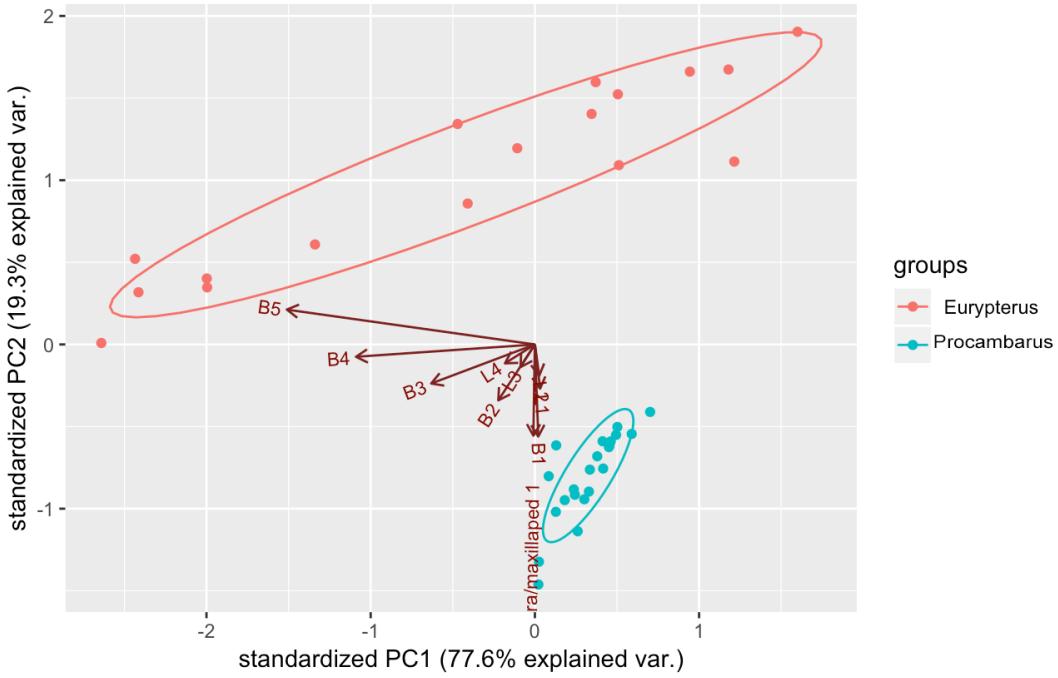

Figure 8: Graph of the PCA of *Eurypterus* and *Procambarus*. X-axis represents the first component. Y-axis is the second component. Minor components shown as maroon vectors in the center. Each point represents the first and second component scores of all measurements of a single specimen. Ovals encompass 90% of the datapoints. The *Eurypterus* data has a large range over the first component, and has a high second component score. *Procambarus* data is tightly clustered around (0,-1).

3D Modelling

The second part of my work involved using 3D modelling as a tool for reconstructing flattened fossils. I scanned one of the most complete of my fossils. The fossil scan was enlarged on the y-axis at 115% to approximate pre-taphonomic conditions. I estimated that the original fossil was only 15-20% taller than the original fossil, which had been compressed significantly.

Moving parts/Range of Motion

Working in 3D also yielded an excellent model for biomechanics. Using Blender, we were able to rig every coxa and the metastoma separately to determine their range of motion. Segments were all articulated separately and rotated on the x-axis, perpendicular to the anterior/posterior axis. Coxa pairs were also articulated together and moved as a unit. Coxa pair 1 (chelicerae) were articulated together with pair 2, as were 2 with 3, 3 with 4, and so on, to see if neighboring segments would change range of motion in the whole.

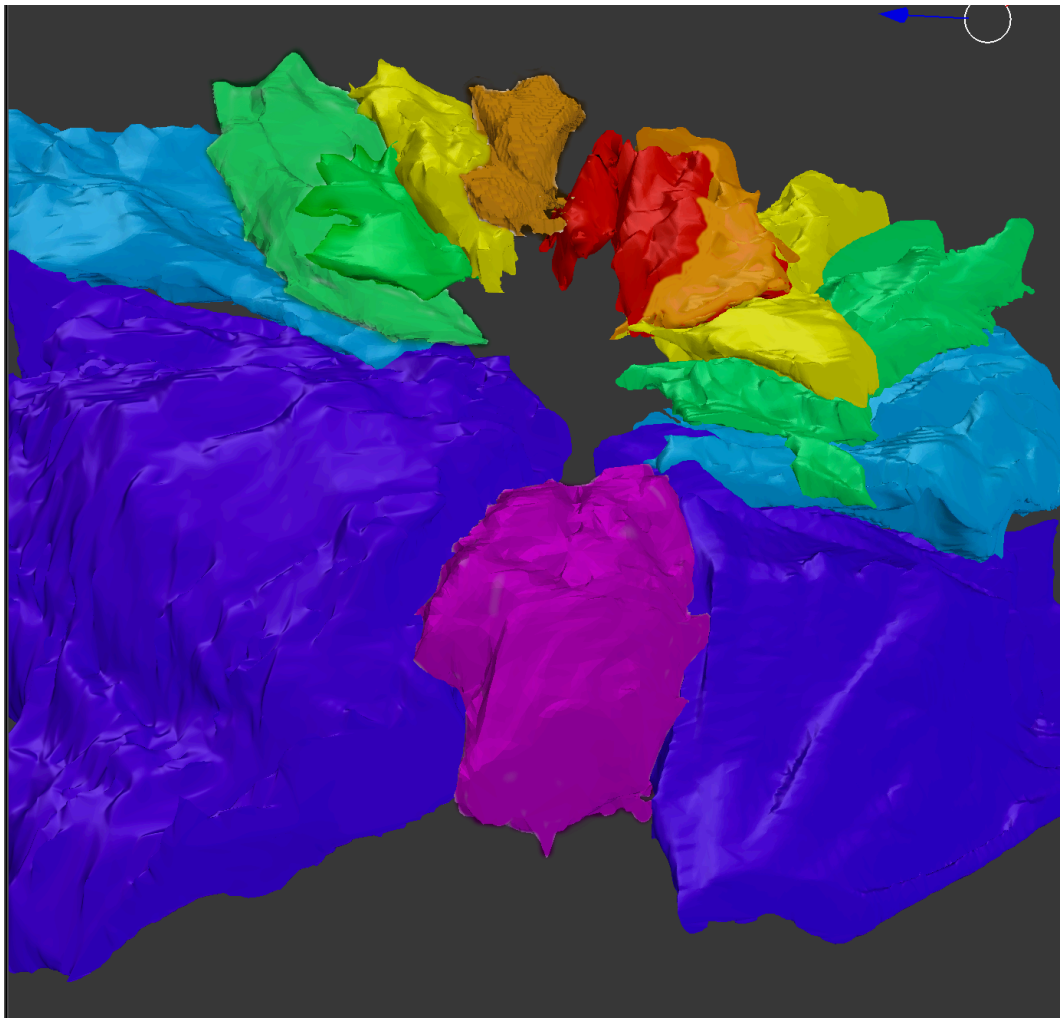

Figure 9: Ventral View of Eurypterus 3D Model. Up is anterior. Chelicerae are in red, first coxae in orange, second in yellow, third in green, fourth in teal. Basipodites in purple. Metastoma in pink. Each colored segment could be articulated separately.

Chelicerae	0.0*
1st Walking Leg	5.3*
2nd Walking Leg	4.8*
3rd Walking Leg	4.5*
4th Walking Leg	5.0*
5th Walking Leg	4.9*
Basipodite	26.3*
Metastoma	24.1*

Basipod movement:
Translate Y -0.110
Translate Z -0.077 mm

Table 1: Degrees of Rotation for Model Coxae. Small table defines basipod movement recorded in mm.

The basipod and metastoma have the biggest range of motion at 27.5°. There is no back of the body in this specimen, so abuttal with the opisthoma could not be determined.

DISCUSSION

Given the lack of correlation between *Procambarus* and *Eurypterus* in my principal component analysis, this study did not find evidence of convergent evolution between the mouthparts of these species. I hypothesized that if there was convergent evolution, I would find an overlap between the principle components explaining the mouthparts. I found no such overlap. No conclusions about *Eurypterus*' diet can be drawn from the comparison of these two species.

However, 3D modelling in this study reconstructs the range of movement of *Eurypterus* mouthparts, which can be used to reconstruct mouth function. I found that Eurypterus had a high degree of movement in its basipodites, which supports Bicknell's analysis that the basipodites provided most of the mechanical power for *Eurypterus* to crush food.

This use of 3D software has implications for its use not only on soft body fossils, but arthropods in general. Recently, it has become fashionable in invertebrate paleontology to scan specimens in the hopes they will contain soft body traces. This project affirms that CT scanning and 3D reconstruction are still useful with fossils that do not show any soft body traces, because it is possible to move segments to establish their potential range of motion.

Principal Component Analysis

The principal component analysis ran well, even though it did not support the hypothesis. My first two components explained the variance in over 98% of the data, indicating high significance of those components.

However, when graphed, the *Procambarus* and *Eurypterus* data did not overlap at all. This meant there was no commonality in degrees of the first two components, and suggests that *Eurypterus* and *Procambarus* have no significant resemblance. The lack of overlap, and lack of convergent evolution, precludes using this comparison to reconstruct the diet of *Eurypterus*. The prevailing theory that *Eurypterus* ate mostly small, live invertebrates remains.

Eurypterus had a larger range of component 1 scores. I believe the first component was mostly size, and this could explain the distribution of component 1 quite well. My fossils ranged from a couple of centimeters to almost a foot (~30 cm) long. Size is often the first component in morphology studies, and could account for the bigger range in *Eurypterus.*

The second component is more mysterious. There was a great difference in component 2 scores between species. Maxilliped /chelicera length is most sharply vertical vector in the cluster in the center of the graph, which suggests that appendage length is important to this axis. This means either the length of the feeding appendage is either less important than I thought, or that these appendages have vastly different lengths, and are not homologous.

Limitations

This thesis was ambitious and novel, so it was less likely to find evidence of convergence between the two species. There was a very slim chance that *Procambarus* and *Eurypterus* would show signs of convergent evolution. Also, as previously discussed, convergent is difficult to identify and measure even in extant organisms, not to mention extinct ones.

There is also the possibility that many morphologies are equally successful in marine detritivores. Perhaps there are multiple feeding strategies that arthropods can employ, and therefore, arthropods will not exhibit convergent evolution to this niche. In short, a "one size fits all" solution may not be possible for *Eurypterus* and *Procambarus* to converge upon. Further study of other marine detritivore arthropods would be required, to see if such an ideal convergent form does exist.

Limitations with Methods

Another issue is simply that my methods could be improved. I could have performed a more comprehensive study with more data and more complex statistics. Another explanation is that taphonomy is interfering with measurement in some way for which I could not account.

My sample size could be expanded. Even considering the Peabody's extensive collections as well as 150 years of literature, only 30 *Eurypterus* specimens could be measured. Of that, I had to cut much of my data, because

specimens were incomplete. Complete exoskeletons are rare, and I could only use fossils that were exposed on the ventral side.

PCA analysis is commonly performed in this field, but may not have had sufficient power to detect the overlap we had predicted. Perhaps another type of multivariate analysis would have been helpful.

Taphonomy may have also been distorting the original fossil itself somewhat, although I think it's unlikely. The preservation is quite good in the Bertie Waterlime, with barely any shear horizontally. My concern is that the feeding appendages may have folded over so only half the length of the chelicera could be measured.

However, there is some debate as to whether *Eurypterus lacustris* actually lived in the environment in which it was preserved. Kjelleswig-Waering (1979) hypothesized that Eurypterus molts and bodies were washed into the near-shore depositional environment from deeper waters. This would disprove my idea that *Procambarus* and *Eurypterus* evolved to fill similar niches. However, there are several other theories as to why live eurypterids would have congregated in the area. A mass molting event or a spawning event could attract *Eurypterus* in the numbers needed to explain the high concentration of fossils. As I found, not all of the fossils are molts. This lends credence to the mass spawning hypothesis.

3D Model

The results from the 3D model were more promising. Modelling in Blender, I could move and rotate the individual coxae to try and see where the limit of motion might be for eurypterids. I moved every segment separately as well as in groups of two, groups of three, and groups of four. I found there was a very tight overlap between the coxae that could not be discerned from the surface fossil. The first four coxae could not be moved towards the center of the mouth significantly without bumping into the other coxae. They had to be moved as a unit. These coxae also could only be rotated an average of 5° before they began to clip through the adjacent segments.

In contrast, the basipodites had an incredible range of motion. They could move anteriorly and in towards the mouth, and could also be rotated 27.5*. This raises the question of the flexibility of Eurypterus. This topic has been breached by Persons and Acorn (2017) in their study on horizontal flexibility in eurypterids. Persons and Acorn described a fossil that curved dramatically to the right on a flat bedding plane. They interpreted this as evidence that the telson could be used in prey capture. Lamsdell et al. (2018) disagreed with their theory, and deemed the fossil a molt. The thin, chitinous coating of a molt could have easily deformed to a posture the arthropod never could have held in life.

Eurypterids are often reconstructed swimming with an up and down undulating motion. *Limulus*, their close living relatives, can roll up so their telson is held about 330 degrees from the prosoma (Fearon, pers. observation). Limulus

use this ability to right themselves when they are knocked prone. Based on the observations of the forebody I have made, Eurypterus may have been able to "roll up" as well. Eurypterids may have been a highly flexible group, at least in an up-and-down motion.

The basipodite range of motion could have generated force for masticating food. Most of Eurypterus' gnathobasids are located on the basipodite, indicating it had a disproportionate role in crushing and carding food. If other segments cannot move to masticate food, calculating the force with which the basipodite strikes the food item could be used as a proxy for the bite force of Eurypterus. This would help model the types of organisms and materials Eurypterus could eat, and could be used to reconstruct diet.

Using this model, I hypothesize that Eurypterus could likely crush thin-shelled organisms such as gastropods, provided they are under about 4 cm. Baltoeurypterus had cuticle reminiscent of Limulus gnathobasids, and it is not unreasonable to assume Eurypterus could have had a similar structure (Bicknell, 2018a). However, the cuticle layers in Baltoeurypterus were thinner than in Limulus, and probably could not handle harder shelly organisms that Limulus may consume (Bicknell, 2018a). In addition, the upwards grinding movement of the basipodites could likely generate a strong enough force to crack shells in the substrate, as well as resisting the wear and tear of large seafloor particle sizes that could enter the mouth.

The very existence of this model also settles a contested point: it confirms that *Eurypterus* bodies were preserved in the Bertie Waterlime, not just molts. Heubusch (1962) proposed that all fossils found in the Bertie Waterlime were actually molts, or exuviae. An exuvium consists of a thin layer of polymerized layer of cuticle, filled with dolomite (Gupta, 2007). The segments found in the 3D model would not be visible if the fossil were only a molt. Our specimen had to have been a corpse. Vrazo (2014) has supported Heubush's hypothesis, although he softened his position to acknowledge that body fossils were present in the Bertie Formation. Distinguishing body fossils from exuviae is notoriously difficult, but has been attempted (Tetlie et al. 2008). Usually, a crack in the cuticle on the ventral side, just below the prosoma is considered evidence of a molt. Vrazo suggested that eurypterids might have congregated in this area to molt. However, with concrete evidence for eurypterid body fossils, there is an argument for *Eurypterus* living in the conditions in which it was preserved. This study also has implications for the use of 3D modelling to identify molts and body fossils.

3D Model Limitations

Since I delineated closely packed segments by hand, there is some overlap in the model, leading to problems with rigging and printing the model, as well as confusion in designating areas of different legs.

Conclusion

I can conclude that with these analyses, *Eurypterus lacustris* and *Procambarus clarkii* do not show evidence of convergent evolution in their mouthparts. Based on the principal components analysis, these arthropods have very different mouth forms. The principle component of mouth shape was mostly size, followed by appendage length.

However, range of motion modelling was very successful with the 3D model. I determined that the first through fifth coxae probably did not have an extensive range of motion, and therefore could not assist significantly in prey capture on mastication. The basipodites, however, exhibited high degrees of movement, indicating that they had enough range of movement to be the primary masticators for Eurypterus. This agrees with the microstructure of the gnathobasids, which are much more developed on the basipodites than elsewhere.

Future Work

In future projects, I want to include a Burnaby-Back projection before my PCA, to factor out size in the analysis. I may get different results without size as a factor, as I think it made up most of my first component.

I will also improve my 3D model by estimating the force the basipodites could exert upon a food item entering the mouth. This could help determine what food items *Eurypterus* might be capable of eating, and assist in a reconstruction of diet.

I will also create a Brownian motion model of the lineages of Malacostraca and *Eurypterina* to model their divergent paths over time. Ornstein-Uhlenbeck modelling allows a quantifiable analysis of evolutionary paths (Cooper, 2016). If the model retraces a convergent path, it is likely that the lineages are convergent. Ornstein-Uhlenbeck modelling is popular, but it does not work well with small datasets (Cooper, 2016). I would hope to expand my dataset with fossils from more collections.

TABLES

Nr.	Paper/Collection	Page_Nr./Coll_Nr.	Species_Name	TL	B1	B2	B3	B4	B5	L1	L2	L3	L4	BL	BB	BQ	ML	MB	MM	Sex?	chelicera
1	yale peabody	212365-ventral (1)	Eurypterus lacustris	146.53		6.36	12.15	26.85	39.71	50.46	3.72	3.14	5.12	9.5	23.14	19.15	27.52	14.55	9.67	13.64 F	7.67
2	yale peabody	208503	Eurypterus lacustris	N/A	N/A	N/A	N/A	N/A		46.32 N/A	N/A	N/A	N/A		13.79	24.14	18.3	16.3	9.43	14.46 n/a	n/a
3	yale peabody	YPM216689	Eurypterus lacustris	N/A	4.94	12.76	24.72	39.18	52.03	2.19	1.61	4.94	9.29	24.1	25.61	28.51	19.31	10.98	18.62 n/a		8.72
4	yale peabody	208503 stitch	Eurypterus lacustris	N/A	N/A	N/A	N/A	N/A	41.48	N/A	N/A	N/A	N/A	16.02	23.87	22.38	16.3	9.87	14.56 n/a		n/a
5	yale peabody	216689	Eurypterus lacustris	N/A	6.51	14.93	27.97	45.29	50.62	2.36	2.26	5.94	6.72	30.09	28.64	39.5	21.73	11.69	21.07 n/a		10.45
6	yale peabody	212364-10547	Eurypterus lacustris	N/A	N/A	N/A	N/A	N/A	41.57	N/A	N/A	N/A	N/A	17.68	17.84	19.16	14.68	8.66	N/A F		N/A
7	yale peabody	212365(2)	Eurypterus lacustris	145.47	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
8	yale peabody	216591	Eurypterus lacustris	149.33	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	21.03	14.48	N/A F		N/A
9	yale peabody	214177/216691	Eurypterus lacustris		N/A	N/A	N/A	23.35	35.56	N/A	N/A	N/A	N/A	17.62	17.02	19.77	12.67	6.49	12.2 M		N/A
10	Harvard	PALI-131863	Eurypterus fischerii	99.87	7.19	12.79	29.6	33.91	44.83	0.69	1.44	3.14	7.15	19.97	21.03	23.87	15.16	9.49	14.6 F		5.71
11	Harvard	PALI-109669	Eurypterus fischerii	N/A	1.86	8.21	14.99	24.05	24.6	1.3	1.06	3.69	7.51	14.75	14.45	15.77	9.39	5.98	9.15 M		6.76
12	Harvard	PALI-132030	Eurypterus lacustris	97.61	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
13	yale peabody	114704	Eurypterus spp??	40.56	1.91	5.95	7.9	13.73	16.56	0.89	1.23	0.77	2.72	8.79	8.35	9.86	6.18	3.49	6.18 M		1.67
14	yale peabody	38866 Detail	Eurypterus spp??	N/A	3.96	6	8.9	7.84	5.48	1.13	0.95	1.27	0.58	6.38	6.14	7.59	5.56	4.43	5.33 M		1.94
15	yale peabody	i3406_2	Eurypterus spp??	N/A	1.59	4.08	8	13.64	19.54	1.08	0.78	2.9	3.27	10.33	9.28	11.35	7.36	4.62	7.19 N/a		2.6
16	yale peabody	i3406_1	Eurypterus spp??	52.37	2.67	6.45	8.79	13.15	19.82	0.3	0.96	1.85	3.17	8.71	9.09	10.9	6.78	4.44	6.69 N/a		3.29
17	Yale peabody	ROO52482	Eurypterus spp??	53.81	N/A	N/A	N/A	N/A	21.18	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A F		N/A
18		MIN Stack	Eurypterus spp??	11.39	N/A	N/A	N/A	N/A	3.56	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A		N/A
19	Yale peabody	208238	Eurypterus lacustris	N/A	5.51	15.14	17.4	25.97	41.3	3	1.36	3	6.68	20.23	20.33	24.44	16.75	9.2	16.65 M		6.95
20	Yale peabody	210956	Eurypterus lacustris	27.68	1.28	3.81	4.67	6.13	9.36	0.68	0.62	0.87	2.03	4.45	3.89	4.91	2.74	2.1	2.74 M		1.52
21	Yale peabody	209392	Eurypterus lacustris	11.98	0.48	1.27	2.37	3.03	4.11	0.25	0.32	0.44	0.65	1.46	1.6	1.54	1.37	0.82	1.32 M		0.65
22	Yale peabody	212426	Eurypterus lacustris	83.78	3.66	7.66	10.05	17.91	25.23	1.02	0.62	2.7	3.94	13.12	11.99	14.34	9.52	3.55	9.23 M		4.86
23	Yale peabody	215288	Eurypterus lacustris	37.3	1.46	3.37	5.62	9.23	11.59	0.11	0.23	1.46	3.49	6.65	5.02	7.08	4.67	2.48	4.67 F		1.78
24	Yale peabody	217769	Eurypterus lacustris		11.37	12.67	19.67	35.51	47.66	2.5	1.36	6.22	7.57	20.65	22.07	25.48	19.15	10.43	17.57 N/A		5.77
25	Poschmann 2006	Fig. 1	ADELOPHTHALMUS SIEVERTSI	60	N/A	N/A	N/A	N/A	24.1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	F	N/A
26	Poschmann 2007	Fig.4	ADELOPHTHALMUS SIEVERTSI	17.28	N/A	N/A	N/A	N/A	10.39	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	F	N/A
29	Yale peabody	YPM_IP_425551_99	Eurypterus lacustris	N/A	2.14	6.58	12.67	23.54	27.9	0.49	1.15	2.72	4.63	28.83	16.85	14.2	10.19	5.56	9.82 N/A		3.98
30	MHC	Dekay 1	Eurypterus remipedes	61.24	4.44	7.74	10.07	13.35	15.54	1.12	2.26	2.32	2.35	6.65	8.87	10.03	5.55	3.37	5.55 m?		2.23
31	MHC	Mirror image	Eurypterus remipedes	114.44	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Table 1: Eurypterid Measurements

Nr.	Paper/Collec	Page_Nr./Co	Species_Name	TL	B1	B2	B3	B4	B5	L1	L2	L3	L4	Maxillaped 1	maxillaped 2	Maxillaped 3	Mandible	Weight	Claw Width	Sex (?)
1	MHC (Whole	1	Procambarus clarkii	94.49	13.34	12.25	14.45	17.7	17.75	4.59	4.41	4.48	5.5	9.98	12.27	22.2	4.43	23.17	11.11	f
2	MHC (Whole	2	Procambarus clarkii	83.34	11.15	11.14	12.25	13.33	12.28	4.45	3.4	3.45	4.4	12.2	12.25	20.12	4.45	16.16	10	m
3	MHC (Whole	3	Procambarus clarkii	94.44	13.3	12.24	14.37	17.75	15.55	4.49	4.45	4.47	4.5	13.34	11.12	16.75	7.76	23.78	14.49	f
4	MHC (Whole	4	Procambarus clarkii	90.1	13.32	11.15	13.36	15.55	15.56	4.4	4.43	5.51	5.52	14.5	15.57	19.94	6.68	20.45	10.02	f
5	MHC (Whole	5	Procambarus clarkii	81.15	12.21	10.07	12.25	14.47	14.42	6.71	5.54	4.45	5.55	11.16	11.19	18.87	5.57	14.59	8.89	f
6	MHC (Whole	6	Procambarus clarkii	103.33	16.64	15.54	16.65	18.85	17.74	7.8	5.55	4.48	6.68	11.61	14.45	25.54	7.74	33.72	16.64	m
7	MHC (Whole	7	Procambarus clarkii	85.54	11.13	10.03	12.26	14.42	14.41	5.51	4.39	3.35	4.51	13.37	14.47	21.15	5.55	18.16	11.12	m
8	MHC (Whole	8	Procambarus clarkii	91.14	13.35	12.25	14.37	15.54	15.54	6.6	3.39	4.46	6.67	13.35	16.61	21.13	8.89	26.24	14.45	m
9	MHC (Whole	9	Procambarus clarkii	101.08	9.44	13.38	15.57	17.8	17.76	5.55	4.46	5.54	6.61	14.48	16.64	26.66	7.76	27.41	13.31	f
10	MHC (Whole	10	Procambarus clarkii	105.53	15.57	15.52	16.6	18.84	17.74	7.73	5.51	5.55	6.71	14.51	15.52	6.63	8.87	26.11	N/A	m
11	MHC (Whole	11	Procambarus clarkii	88.92	11.14	10.1	12.25	14.47	14.41	5.51	4.4	4.43	5.57	13.33	14.48	20.05	8.88	15.92	N/A	f
12	MHC (Whole	12	Procambarus clarkii	91.08	13.3	12.24	14.45	17.7	16.68	4.51	4.44	5.51	4.41	14.45	16.59	21.15	7.82	18.8	N/A	f
13	MHC (Whole	13	Procambarus clarkii	87.73	12.24	11.18	13.34	15.57	15.51	5.51	4.45	4.42	5.5	13.35	12.2	20.08	7.79	15.95	N/A	f
14	MHC (Whole	14	Procambarus clarkii	91.11	11.18	12.2	13.37	15.52	14.49	4.47	3.35	4.4	4.47	13.32	13.35	18.81	8.82	15.77	N/A	f
15	MHC (Whole	15	Procambarus clarkii	81.2	10	10.08	11.21	12.28	11.21	4.47	3.4	3.38	4.44	12.25	10.05	18.8	4.47	10.77	5.51	f
16	MHC (Whole	16	Procambarus clarkii	85.51	12.29	13.33	15.5	16.65	15.58	5.52	4.47	4.45	4.5	13.34	13.3	21.21	6.6	19.17	10.11	f
17	MHC (Whole	17	Procambarus clarkii	95.56	12.23	13.33	14.5	18.85	16.64	6.62	4.43	4.45	6.69	14.47	15.6	24.42	7.7	19.24	N/A	f
18	MHC (Whole	18	Procambarus clarkii	82.24	12.24	11.15	12.3	15.55	14.45	4.49	3.38	3.4	4.5	12.23	12.22	20.11	6.62	12.64	N/A	f
19	MHC (Whole	19	Procambarus clarkii	97.81	14.44	12.29	14.44	16.65	15.59	6.64	4.48	4.49	6.68	14.48	15.54	13.41	6.72	20.69	N/A	m
20	MHC (Whole	20	Procambarus clarkii	83.4	11.18	11.14	12.3	14.45	13.34	5.52	4.43	4.42	5.56	11.14	12.3	21.17	6.61	17.16	9.95	m
21	MHC (Whole	21	Procambarus clarkii	84.49	11.14	10.01	12.26	14.46	13.34	5.51	4.4	4.43	5.55	11.2	9.92	18.85	6.68	13.83	N/A	m
22	MHC (Whole	22	Procambarus clarkii	85.56	12.22	11.19	13.37	14.49	14.52	5.53	3.38	4.44	5.53	13.37	14.42	16.66	5.54	18.09	9.95	f

Table 2: Crayfish Measurements.

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                Comp.1 Comp.2 Comp.3 Comp.4 Comp.5 Comp.6 Comp.7 Comp.8 Comp.9 Comp.10
SS loadings      1.000  1.000  1.000  1.000  1.000  1.000  1.000  1.000  1.000   1.000
Proportion Var   0.067  0.067  0.067  0.067  0.067  0.067  0.067  0.067  0.067   0.067
Cumulative Var   0.067  0.133  0.200  0.267  0.333  0.400  0.467  0.533  0.600   0.667
                Comp.11 Comp.12 Comp.13 Comp.14 Comp.15
SS loadings       1.000   1.000   1.000   1.000   1.000
Proportion Var    0.067   0.067   0.067   0.067   0.067
Cumulative Var    0.733   0.800   0.867   0.933   1.000
> summary(combined.pca)
Importance of components:
                          Comp.1    Comp.2      Comp.3      Comp.4      Comp.5      Comp.6
Standard deviation     16.230427 8.1012736 1.834383833 1.656470946 1.262868774 1.025475463
Proportion of Variance  0.776016 0.1933381 0.009912682 0.008083108 0.004698154 0.003097857
Cumulative Proportion   0.776016 0.9693540 0.979266716 0.987349825 0.992047978 0.995145835
                           Comp.7      Comp.8       Comp.9      Comp.10
Standard deviation     0.952193363 0.614333675 0.4887765718 0.3532940725
Proportion of Variance 0.002670921 0.001111781 0.0007037713 0.0003676914
Cumulative Proportion  0.997816756 0.998928537 0.9996323086 1.0000000000
```

Table 3: Raw Principal Component Data. Proportion of variance indicates how much influence that component exerts over the data.

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