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Power Amplification Strategies Across Animals

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Evolution of Power Amplification Methods

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Abstract

Animals use muscles for movement, but some have evolved mechanisms to exceed maximum power used in a motion known as power amplification. In this literature review, I analyzed and compared the evolution of structures capable of power amplification between species. Structures capable of power amplification were broken down into the basic components of the engine, amplifier, and tool. The species analyzed were found to possess necessary structures for power amplification which were relatively similar to each other in morphology, but varied greatly in function. The ease with which these structures evolved was evaluated based on the amount of divergence which occurred in the organisms, and convergent evolution across clades. The complexity of the structural modifications and components needed to perform power amplification was not the same across species. While there is some insight on the evolution of power-amplified structures, overall, more research needs to be done in determining the rate of evolutionary change.

Key Words: Evolution, Power amplification, *Stomatopoda*, Trap-jaw ants, *Mecysmaucheniidae, Macroramphosus scolopax*, Sculpins

Introduction

Power Amplification

Much of how animals move is powered by muscles. Muscles are powered by enzymatic processes which cause the actin-myosin crossbridge cycle to occur, causing muscle contraction. The amount of power that a muscle can exert is limited by the rate of the enzymatic processes. As the maximum power through muscles is constant, there is a tradeoff between force and velocity where an animal can use great amounts of force but slowly, or an animal can use small amounts of force at high velocity. However, this amount of power is not enough to perform movements like the jump of a frog which uses launches itself in the air as a projectile over 40 times its body length, which needs force but also high speed.

Power amplification is a way that power can be increased past regular muscular levels. In animals, power amplification can perform fast, powerful movements which would be normally impossible through normal muscle power. Generally, these mechanisms occur only in smaller organisms since in larger organisms, a larger muscle mass means they can generate large amounts of power without needing a power-amplified system. Power amplified systems work through an elastic medium. This material must be able to store large amounts of energy so that it is later exerted on something. The system must also include a catch mechanism where, when the system is caught, energy is instead put into the elastic material. Finally, the system must include a mechanism which undoes the latch and allows the large amount of energy to be used at once. The force is the same as a muscle would have provided, but the time it takes to use that force is shorter, meaning it has a faster velocity and thus greater power. This mechanism can provide a diverse range of benefits for an animal that uses it: some animals use power amplification for prey capture like trap-jaw spiders, some for jumping like fleas, and some for being able to destroy the hard shell of prey, like mantis shrimp.

Evolution

The many components in power amplification bring up questions about how these structures evolved. The evolution of certain components like latch mechanisms are not favorable alone as they often serve no purpose. Components which are harder to evolve only are found rarely, whereas components which are easier to evolve will have convergently evolved multiple times. While power amplification produces a movement that cannot be matched by the regular movement of muscle, it has its drawbacks and limitations as well. The system by which the power amplification typically functions only allows for a forceful movement in one direction. This means that, although power amplified mechanisms are in great diversity across species, one organism does not possess all of their strength from these. In effect, power amplification uses a great amount of energy for a task that has a lack of feedback. Instead, situations where power amplification is helpful are generally where speed is necessary. Hunting is one of these situations, with the predator and the prey wanting to beat the other in getting captured or not.

Phylogenetic Comparative Methods

The key to determining what kind of adaptations took place in history is to compare how closely an organism is related to others. While it may be useful to compare one species to another, this does not help in determining the complexities in dealing with a larger number of species' differences. Looking at the genes of a species is the most accurate way to determine how one species differs from others. The numbers of differences are obtained and used in constructing a phylogenetic tree. Maximum parsimony can be used, and from there, a rough outline of how organisms descended from common ancestors can be obtained. Independence is assumed in traditional statistics, such as simple regressions across many species. However, all species are part of an ordered phylogeny so independence does not exist. Felsenstein developed a phylogenetic comparative method which can account for nonindependence of taxa, which requires previous knowledge of the topology and branch lengths to be corrected. It uses the rate of Brownian motion as a model, which is based on random displacement of suspended molecules. The expected constrast is compared with the actual constrast, resulting in variances that can be calculated for each branch compared to another. From this, the phylogeny can be reconstructed with more accurate topology and branch lengths. The biggest drawback of this system is that the constrasts must be obtained, and those sources are limited to gene frequencies, gene sequences, and qualitative characteristics. If phylogenies are not taken into account, comparisons between species lose their evolutionary basis. Homologous structures alone cannot signify if an two organisms have the potential to adapt the same way.

The power-amplified structures explored in this review are the raptorial appendage in *Stomatopoda*, the mandible in trap-jaw ants, the chelicerae in *Mecysmaucheniidae* (trap-jaw spiders) and the snout in Snipefish. The jaw of Sculpins have potential to become amplified, and are examined as well.

Morphology of the Raptorial Appendage in Stomatopoda

Stomatopoda, commonly known as Mantis Shrimps, are an order of crustaceans which have evolved a powerful second pair of thoracic appendages which can be used to spear or smash prey. [1] These appendages can be broken down into a simple model which allows for power amplification: a part which creates the large amount of force, known as the engine, the part known as the amplifier which does the amplification similar to a spring, and the part that moves rapidly as a result of this, known as a tool. [7] The engine in power amplification in *Stomatopoda* is the lateral extensor muscle. [7] The amplifier is the dorsoventral part of the distal part of the merus, referred to as the meral-V structure. [7] The tool consists of the propodus and dactylus. [7] In effect, the raptorial appendage is a four-bar linkage system. On some of the dactyli, there are barbed tips which make the organism a spearer, whereas those without barbs on the dactyli are smashers. Spearers use their dactyli for impaling prey, whereas smashers use theirs for destroying exoskeletons.

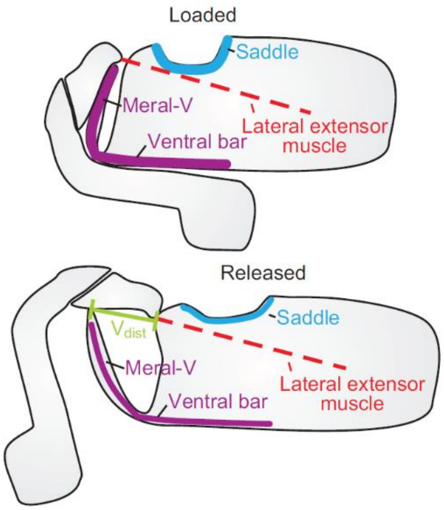

Figure 1. Loaded and released states of *Stomatopoda* appendage. The lateral extensor muscle is responsible for the generation of power, and the meral-V and saddle structures are responsible for elastic energy storage.

From Patek et al. 2013.

Evolution of Raptorial Appendages

The power amplification in raptorial appendages in *Stomatopoda* likely evolved only once, with no family of *Stomatopoda* having lost this function over time. Ahyong found that within the superfamily Gonodactyloidea, *Protosquillidae*, *Odontodactylidae*, *Gonodactylidae*, and *Takuidae* all possess subterminal ischiomeral articulations of the raptorial appendage which allow them to perform an even more forceful power amplification. [1] The outgroups *Alainoquillidae*, *Pseudosquillidae*, and *Hemisquillidae* do not have these adaptations. Patek et al. found that *Hemisquillidae* are undifferentiated in regards to if

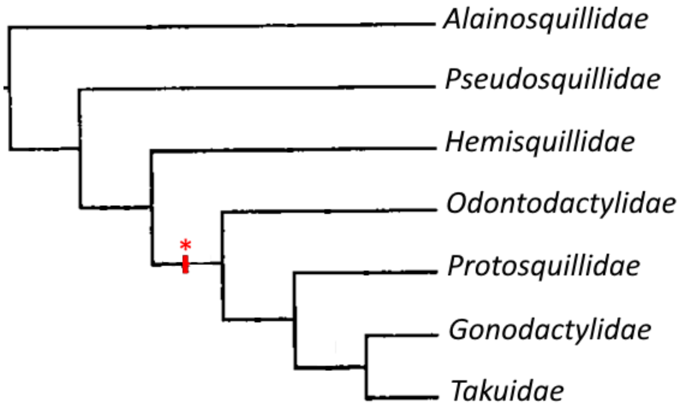

Figure 2. Cladogram of Gonodactyloidea based on maximum parsimony, with asterisk denoting where subterminal ischiomeral articulations likely evolved.

Modified from Ahyong 1997.

they are spearers or smashers. [22] The families *Pseudosquillidae, Lysiosquillidae,* and *Squillidae* were all found to have features more similar to spearers, while *Gonodactylidae* were found to have features more similar to smashers. [22] As Ahyong described, *Pseudosquillidae* and *Gonodactylidae* are more closely related to each other as Gonodactyloidea than they are to *Lysiosquillidae* and *Squillidae*; thus, spearing either evolved multiple times, [8,22] or the subterminal ischiomeral articulations evolved multiple times. [1] Because we know *Hemisquillidae,* another member of the Gonodactyloidea superfamily, are undifferentiated, the undifferentiation also potentially evolved multiple times in *Stomatopoda* evolutionary history.

Claverie et al. analyzed seven fossils of *Stomatopoda* which were ancestors to the modern families and used them to calibrate a phylogeny to support their hypothesis that spearer and smasher functionality only evolved once. [7] They used that fact that as the body scaled in size, the elastic system scaled positively. Homologous structures were also considered when analyzing the fossils and matching them to current species. Finally, the spring force used by these organisms that are spearers vs smashers was found to be correlated with a greater amount of speed and acceleration.

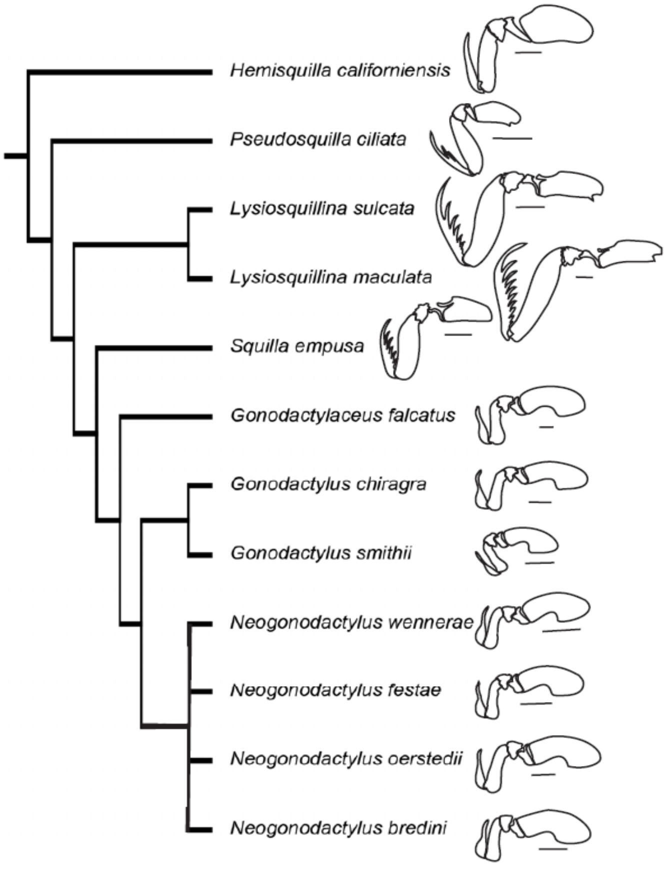

Figure 3. Cladogram of the undifferentiated *Hemisquillidae* with spearers *Pseudosquillidae*, *Lysiosquillidae*, and *Squillidae*, and smashers *Gonodactylae* and *Neogonodactylae*.

From Patek et al. 2013.

Morphology of Mandibles in Trap-Jaw Ants

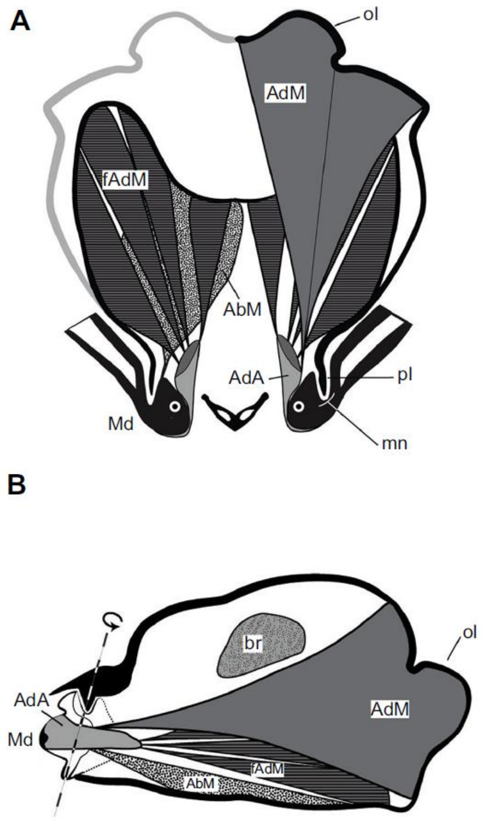

Figure 4. Morphology of the head of *Myrmoteras Iriodum*. fAdM is the fast mandible closer muscle, Md the mandible, and mn the mandibular notch. (A) Dorsal view, (B) Saggital section

Modified from Larabee et al. 2017.

Trap-jaw ants are species of ants which possess a mandible with rapid closure due to the release of a latch mechanism. They use power amplification for quick prey capture. There is a wide diversity of mandibles capable of power amplification, as trap-jaw ants do not form a monophyletic group. [16] Trap-jaw ants have trigger hairs which, when stimulated, cause the power amplified mandible closing mechanism to occur. [11] Within the subfamily Ponerinae, trap-jaws have been observed in *Anochetus* and *Odontomachus*, within the subfamily Formincinae, in *Myrmoteras*, and within the subfamily Myrmicinae, in the tribe Dacetini. [16] Trap-jaws may have also evolved in other species whose morphologies have not yet been studied. [16] In *Odontomachus* and *Anochetus*, it has been discovered that the mandible joint is responsible for the latch, and the trigger muscle is the mandible adductor. [16] For the Dacetini tribe, *Acanthognathus* was observed to use a mandibular process as a latch, and a mandible adductor was the trigger muscle. [16] In *Daceton* and *Strumigenys*, the latch is the labrum, and the trigger muscle is the labral adductor. [16] In all studied species, an adductor apodeme was most likely responsible for the elastic energy storage.

Evolution of Trap-Jaw Ant Mandibles

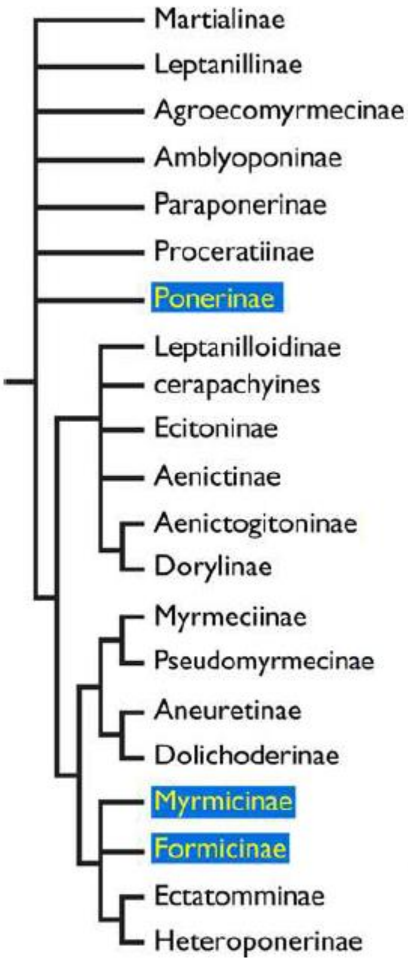

Figure 5. Cladogram of ant subfamilies; those with species which have trap-jaws highlighted

From Larabee and Suarez 2014.

The mechanism for power amplification in trap-jaw ant mandibles has independently evolved at least four times across all ants. Through molecular phylogenetics, it has been suggested that *Anochetus* and *Odontomachus* should be part of the same *Odontomachus* genus group, as they are more similar to each other than other Ponerinae. [16] Other genera in the *Odontomachus* group have not been found to possess trap-jaws, so it is possible that *Anochetus* and *Odontomachus* evolved their systems separately from each other; however, other morphological characteristics in the two genera are quite similar and it has been suggested that *Anochetus* and *Odontomachus* should be in the same clade, thus their systems evolved only once. The tribe Dacetini in subfamily Myrmicinae has a large number of species with power amplified mandibles, although not all have this adaptation. Larabee and Suarez believe that the classification of Dacetini as a tribe is unstable, with them being too diverse to be considered a single clade. Thus, it is difficult to spot where and if there was a single origin of trap-jaws. [16] Using the current phylogeny, it was determined that power amplification in mandibles had evolved multiple times in Dacetini. [16] The subfamily Formicinae has not been studied extensively, and although 34 species have found to possess the trap-jaw mechanism, their mechanisms are vastly different from those found in Ponerinae and Myrmicinae. [16]

Morphology of Chelicerae in Mecysmaucheniidae

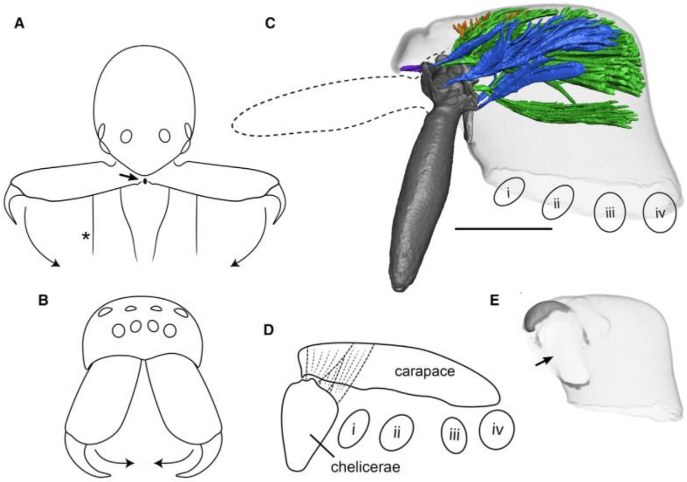

Figure 6. (A) Dorsal view of a *Mecysmaucheniid* head. (B) Anterior view of a typical spider head. (C and E) Lateral view of carapace in *Zearchaea*, with dashed line showing chelicerae after a strike. (D) Lateral view of typical spider carapace.

From Wood et al. 2016.

Mecysmaucheniidae are a family of spiders, some of which possess a power amplification system in their chelicerae. They use their chelicerae to capture prey by hunting, instead of building a web. Most chelicerae in spiders are controlled by only a few muscles, whereas it has been discovered in *Mecysmaucheniidae* that there is a much larger number of fibers and muscles which increase the jaws' maneuverability. [29] In order to use this maneuverability, however, there also needs to be a modification in the carapace of the spider to accommodate the wider range that the spider can strike with. [29] This has been observed along with a thicker clypeus and clypeal apodemes. [29] These need to be thicker to house the muscles and tendons which power the power amplification mechanism. [29] While it has not been proven what causes the mechanism to work, it has been hypothesized that the anterior outer muscles, the ICS muscles, and the anterior medial muscles are responsible. [28] When the anterior medial muscles contract, great power allows the chelicerae to be moved back, likely making it the "engine" of the system. [28] The contraction of the anterior outer muscles act as a lever arm, allowing the chelicerae to lift up, allowing them to detach from the latch mechanism. [28] The ICS muscles are connected to a sclerite which forms a hinge, causing the closing of the jaw. [28] Four setae are found on the inside of the chelicerae which trigger the system when touched. [29]

Evolution of Mecysmaucheniid Chelicerae

Although *Mecysmaucheniid* are the only spiders that are known to have power amplification in their chelicerae, not all extant species have it. When observed in the existing phylogeny (Figure 7), it appears that the ability to have a power-amplified strike evolved 4 separate times in history through parallel evolution. [29] Measurements of clypeus thickness as a ratio to cuticle thickness showed that power-amplified species have a greater thickness, with the lowest out of the power amplified organisms being slightly higher than the highest of the non-power amplified species. [29] This also holds true for the ratio of the thickness of the clypeal tendons to the cuticle thickness. [29] So, while some species have a similar clypeal thickness, they do not have a mechanism of power amplification, suggesting that the thickness possibly evolved first, as they are necessary modifications for power amplification in the

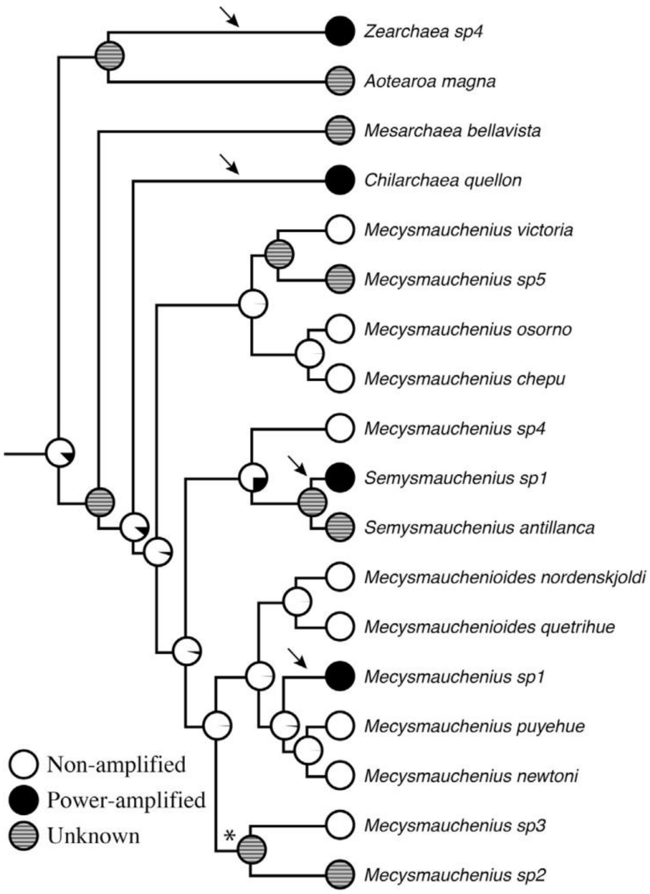

Figure 7. Cladogram of *Mecysmaucheniid* species that shows which are capable of power-amplified strikes. Arrows point to areas where it is hypothesized power amplification evolved.

From Wood et al. 2016.

chelicerae to be possible. The average strike duration, speed, and power output, were all much higher in power amplified species than non-power amplified species, as expected. [29] It has been suggested that hydraulic pressure is responsible for the movement of the anterior outer muscles, which undo the latch mechanic. [28] It was found that leg extension in some spiders is replaced by a hydraulic system using hemolymph pressure to move. [28] After snapping its chelicerae, they stay in an upward confguration (Figure 6, C), and are not re-attached to the latch. [28] Further supporting evidence for this hypothesis maintains that the hydraulic pressure would be able to produce enough force to undo the latch; in the family *Aotearoa*, the chelicerae are so big that the effort used by the anterior outer muscles alone would not be enough. [28]

Morphology of the Snout and Head in Macroramphosus scolopax

Macroramphosus scolopax, commonly known as the snipefish, is a species which has evolved power amplification in its snout, used for pivot feeding. A relative of the seahorse, snipefish have a long snout which they rotate upwards quickly to get close to the prey, and then use suction to capture it. Mechanisms for seahorses and pipefish have been found to use elastic recoil as a way to more quickly rotate their head. [17] There is most likely a four-bar linkage system which allows the movement of the snout to be coupled with the movement of the hyoid, which is responsible for the suction. [17] The anterior vertebrae of *Macroramphosus scolopax* are fused together, allowing them to be highly reinforced. [17] The linkages that make up the four-bar system are the hyoid linkage, a neurocranium to suspensorium link, a urohyal to sternohyoideus link, and a pectoral link which does not move. [17] To perform the snout rotation and suction, the neurocranium-suspensorium link moves from overlapping to not overlapping the urohyal-sternohyoideus link, accommodated with movement of the hyoid. [17] It is hypothesized that when the overlap occurs, a latch prevents movement, and energy can be stored in epaxial muscles. [17] These epaxial muscles cause the neurocranium-suspensorium link to rotate when the latch is not in place, thus making it the engine of this system. The release mechanism comes through the way that the four-bar linkage system works, with the head rotating when the neurocranium-suspensorium link rotates upwards. The amplifier is in the epaxial tendon itself. The tool is the snout, which can quickly rotate and perform suction feeding. The latch is also hypothesized to not be a trigger mechanism but instead uses the hyoid linkage to rotate counter to how they would if the jaw was to move up normally. [17]

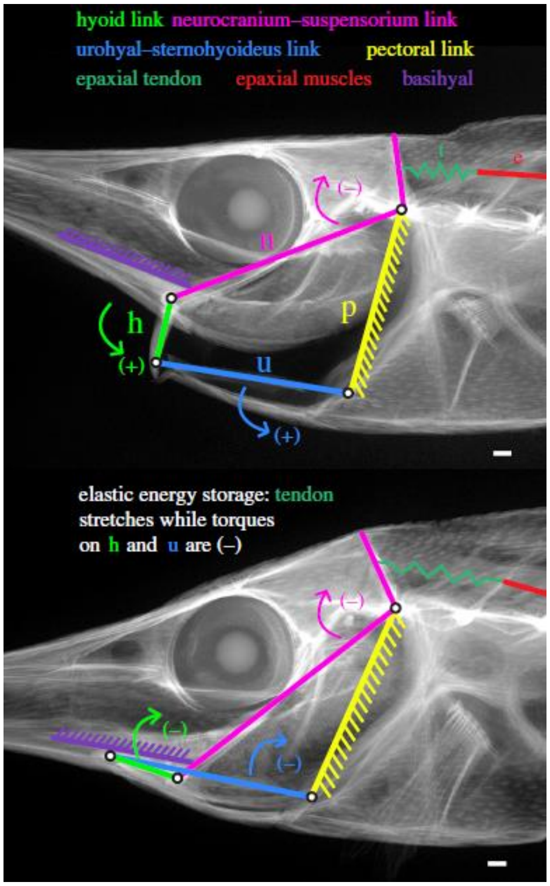

Figure 8. Elastic system in *Maroramphosus scolopax*. Top image shows snipefish with extended snout, bottom image in resting state.

Modified from Longo et al. 2018.

Evolution of Macroramphosus scolopax Snout

As it is unknown whether all *Syngathiformes* use power amplification in their snouts, it is difficult to determine at what point the elastic system evolved. [17] So far, we know that pipefish and seahorses have evolved power amplification, as well as snipefish; however,

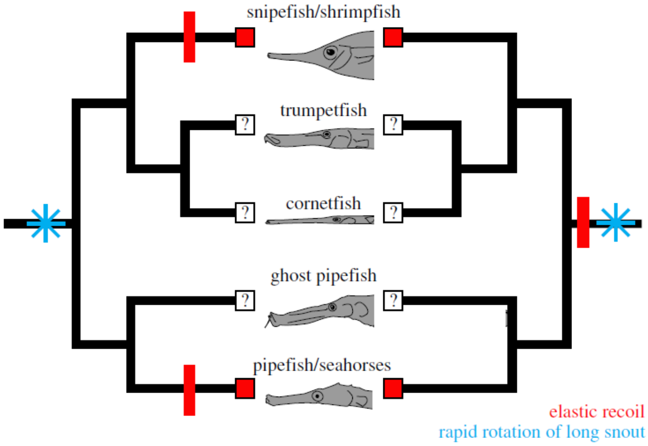

Figure 9. Left and right show two possible points where the elastic recoil mechanism may have evolved due to unknown mechanisms in trumpetfish, cornetfish, and ghost pipefish.

From Longo et al. 2018.

through the current phylogeny, this would mean that if any the other species does not all possess power amplification methods, the system had to have evolved or devolved more than once. [17] When viewing the differences in snipefish and pipefish morphology, it could hint at parallel evolution due to there being a similarly shaped four-bar linkage, but the linkages are connected to different structures. Alternatively, the differences could have formed through divergent evolution.

Sculpin Jaw Morphology and Lever Systems

Sculpins are a type of fish which possess lever systems which are potentially capable of making it to power amplification in its jaw. [24] The sculpin's jaw uses a four-bar linkage system with the jaw closing being where power amplification could occur in the evolutionary future. [24] There has been no structure identified as a potential latch for the muscles to hold on to, although with the jaw morphology, it could be similar to the snipefish where there is no latch but instead, the linkages cross over each other, preventing movement when forces are applied. [24] The elastic power would be stored between the jaw muscle and the jaw lever. [24] The powerful jaw muscle would be able to provide and maintain force, as the direction it is pulling in would not disrupt the latch. [24]

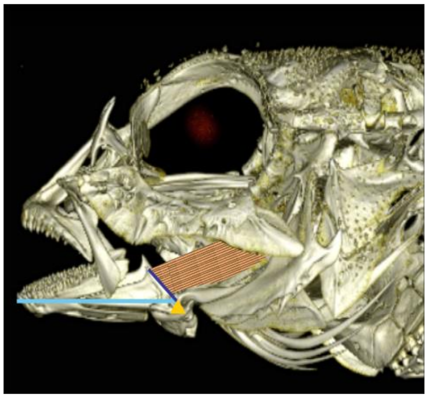

Figure 10. Morphology of sculpin jaw. Powerful jaw muscles are in orange, and jaw is shown with light blue line. Dark blue line shows a potential site for elasticity.

From Roberts et al. 2018.

Evolution of Sculpin Jaw

Sculpins are a group of organisms within the suborder Cottoidei, and consisting of numerous families. In sculpins, there has been no evolution yet of any power amplified methods. However, a larger In:Out lever length ratio generally means that the organism is trying to adapt to be able to use less power while still using a great amount of force, which in turn, could lead to evolving a power amplified method instead. [24] Coupled with the potential for a latch system to evolve from the four-bar linkage and the large jaw muscles, the possible power amplified jaw system would allow the sculpin to snap its jaw shut with immense force and speed.

Controversies

With power amplification methods in many organisms being studied, effort is often put into trying to determine where in the phylogeny such a system evolved. Larabee and Suarez had found issues with the tribe of ants Dacetini, as they claimed it was too broad of a category and the morphological similarities did not match up to the species being related to each other, especially when it came to power amplification. [16] So, with the phylogeny that could potentially be flawed in mind, the conclusion that was developed was that power amplification evolved multiple times, whereas in actuality it may have been far fewer times. [16] Another issue is the lack of a study focusing on power amplified methods in certain organisms related to ones we already know use such a system. [17] This is crucial to finding out exactly where power amplification may have evolved.

Conclusion

Power amplification methods evolved for organisms to be able to perform movements faster than they could with regular muscle power. In the mantis shrimp, this allowed it to provide force to its raptorial appendage. [22] This raptorial appendage evolved only once in mantis shrimp, and all use some form of amplification. [22] The undifferentiated appendages evolved into spearers and, later, smashers. Within all of the different species of mantis shrimp, clades were still preserved. [22] The mandibles of trap-jaw ants evolved numerous times within ant species, despite having evolved the first time after mantis shrimp evolved their power amplification. [16,22] This brings up the question of if mantis shrimp had power amplification that was so evolutionarily effective that it was never lost and instead allowed the shrimp to diversify even more, whereas the power amplification in trap-jaw ants is not as effective so it evolved and then possibly loss of function occurred in descendants. [16,22] This would be the case if it was found that an ancestor of the ants had evolved power amplification. So far, trap-jaw spiders have only been observed in a few species and may have evolved just once. [29] However, there has not been any estimate on how long ago these spiders evolved. It is also unknown when snipefish evolved, and the lack of data on whether snipefish relatives use power amplification makes comparisons of how the different organisms evolved difficult. [17] From the estimates of when seahorses evolved, snipefish have not had power amplified snouts if mantis shrimp; yet both have not had any of its descendants lose the power amplified function yet. [17] The known lack of loss of function would imply that the mantis shrimp's strike is evolutionarily favorable, and that it may be difficult to evolve out of the system, just as it would be difficult to evolve the system. In addition, the diversity in structures in mantis shrimp may have come about through adaptive radiation. Because there were different niches to fill in prey choice, spearers, smashers, and undifferentiated raptorial appendages could have evolved rapidly. Sculpins are an interesting case as some species seem to have a selective pressure on a longer jaw lever arm. [24] A longer lever arm is observed in many other power-amplified systems to provide more power to the system. This also brings up questions of how each organism evolved such a system. The single evolutionary point of the mantis shrimp suggests that it was difficult for the system to come about. Trap -jaw spiders not only need to have the three components necessary for power amplification but also enough to have a modified carapace that allows for the wide cheliceral pre-snap state. [29] However, it is hypothesized, through the differences in carapace shape, these modifications are easy to occur. [29] The trap-jaw mechanism has evolved multiple convergent times as a result. [29] Trap-jaw ants also are hypothesized to have evolved multiple times, and the great variation of mandibles is evidence that the power-amplified system could evolve in differently structured mandibles: another system that is simple to evolve. [16]

All of these systems are similar by design with an engine, amplifier, and tool portion. The lateral extensor muscle in mantis shrimp is a large muscle which produces high amounts of force. For the engine in the various trap-jaw ants, the concept is the same. [16] The engines in trap-jaw spiders and snipefish are also large muscles. If the sculpin had evolved power amplification, it would also use its jaw muscle as an engine as it fits the same things as the features in the other animals. The amplifier in the mantis shrimp is found in the distal part of the merus, where it is able to store force. [22] In trap-jaw ants and trap-jaw spiders, there is a similar muscle responsible for holding force and thus allowing latch opening and closing. [16,29] In the snipefish, the amplifier is actually found in the epaxial tendon. [17] If the sculpin had evolved power amplification, it too would likely use something similar to what the snipefish uses. Finally, for the tool, there is the most variation. The mantis shrimp has multiple functions for its dactyl. [22] Trap-jaw ants and spiders have the same function in snapping closed and causing prey capture. [16,29] Snipefish have a function of not only quickly shifting its snout upwards but also causing a suction effect to occur at the same time. [17] Sculpin would use their bottom jaw as a “tool” to quickly snap their jaws closed. [24]

In all, more research needs to be done in uncovering which animals use power amplification and phylogenetic trees should be updated to get a better understanding of how power-amplified mechanisms evolve. For the mantis shrimp, the oldest example covered in this review, there are still species existing which are undifferentiated in usage of their raptorial appendages. [22] This points to likely being the one of the earliest extant mantis shrimp with power amplified mechanics. [22] Despite this, it is impossible to work backwards and determine which parts of the shrimp's appendages evolved first, or if it was a gradual change at all. [22] On the other hand, the paraphyletic trap-jaw ants, despite having evolved the power amplified mandibles multiple times, we do not have much data about. [16] For certain clades of trap-jaw ants, we have not even discovered the morphology responsible. [16] With trap-jaw spiders, there have been studies detailing certain differences in morphology, which allow us to determine what things are necessary for the power amplification to occur. [28] Directly from the studies, the clypeus and clypeal tendons needed to become thicker in order to accommodate the amount of extra muscle fiber for controlling the latch mechanism. [29] While we have a good hypothesis on how snipefish evolved their power amplified snout and head, we do not know enough about the snipefish's relatives. [17] It is entirely possible that snipefish evolved their power amplification separately from seahorses, and possible that the feature evolved in a common ancestor. [17] There is no real consensus on how these systems evolved, only that they rarely have variation in how their parts work, despite massive variation in what functions they can perform. The result of all power amplification is still the same though: to provide a quick, forceful movement.

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