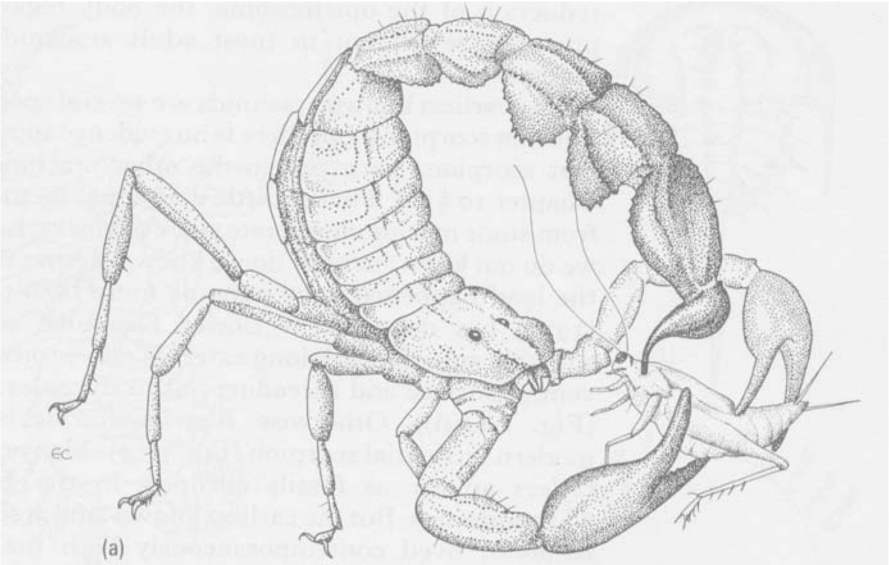
Arthropod Grasping and Manipulation
A Literature Review



Aaron M. Dollar
Harvard BioRobotics Laboratory Technical Report
Department of Engineering and Applied Sciences
Harvard University
April 5, 2001
www.biorobotics.harvard.edu

Introduction

The purpose of this review is to report on the existing literature on the subject of arthropod grasping and manipulation. In order to gain a proper understanding of the state of the knowledge in this rather broad topic, it is necessary and appropriate to take a step backwards and become familiar with the basics of entomology and arthropod physiology. Once these principles have been understood it will then be possible to proceed towards the more specific literature that has been published in the field.

The structure of the review follows this strategy. General background information will be presented first, followed by successively more specific topics, and ending with a review of the refereed journal articles related to arthropod grasping and manipulation.

Background

The phylum Arthropoda is the largest of the phyla, and includes all animals that have an exoskeleton, a segmented body in series, and six or more jointed legs. There are nine classes within the phylum, five of which the average human is relatively familiar with – insects, arachnids, crustaceans, centipedes, and millipedes. Of all known species of animals on the planet, 82% are arthropods (c. 980,000 species)! And this number just reflects the known species. Estimates put the number of arthropod species remaining to be discovered and named at around 9-30 million, or 10-30 times more than are currently known. And this is just the number of *species*; the population of each is another matter altogether. For instance, the mass of all of the ants on the earth is far greater than the mass of all the humans on the earth! [Waldbauer, 1998]

Typically, the naming of arthropods follows the Linnean system of classification, in which each species is given two names: generic (genus) and specific (species). This classification system will be used in this paper, although the common names will be given wherever appropriate. There are, however, many different levels in the hierarchy of taxonomy, of which genus and species are the final two. The following table attempts to describe this hierarchy:

Taxonomic Category	Corresponding Suffix
Kingdom	
Phylum (e.g. Arthropoda)	
Class (e.g. Insecta)	
Order	~oidea
-Suborder	~idae
-Superfamily	~inae
Family	~ini
-Subfamily	
-Tribe	
Genus	
-Subgenus	
Species	

Table 1: Taxonomic classification for arthropods [Romoser, Stoffolano, 1998, and Gullan, Cranston, 2000]

Before proceeding to the relevant anatomy, it should be mentioned that within these many subcategories, a relatively small number of species possess the ability to grasp and manipulate objects in a manner somewhat similar to the human function. Most arthropod legs are only used for locomotion and possibly attachment, whereas capturing and manipulating food sources is typically performed using highly specialized mouthparts. The class of crustaceans contains the most significant portion of those species that grasp and manipulate objects similar to humans. Also significant in this respect are a number of species of the mantids, such as the praying mantis. The published literature on arthropod grasping and manipulation is the richest concerning these two main groups.

Relevant Anatomy and Physiology

General anatomy of insect legs will be discussed first in this section. This is appropriate as most arthropod "grippers" or "hands" are simply modifed legs that have evolved to their present state and use. The basic anatomy is much the same.

Figure 1 below shows a generalized insect leg. The shape and number of the segments in the leg may vary from species to species, and the naming of each seems rather arbitrary. However, the basic structure is remarkably similar across the thousands of different species.

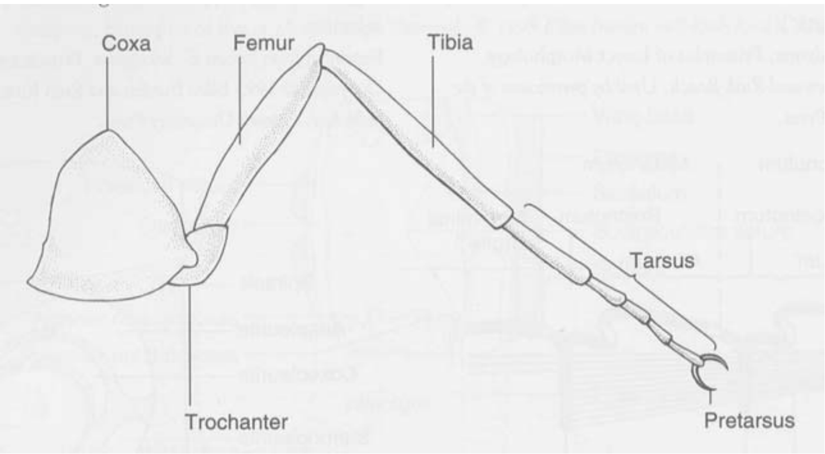


Figure 1: Generalized insect leg [Romoser, Stoffolano, 1998, p.28]

The coxa and trochanter can be thought of as the 'hip' of the insect, the femur and tibia the same as their human counterparts, and the tarsus and pretarsus (or post-tarsus, depending on the classification scheme (distal or proximal)) as the foot and toes. It is in these last two areas that the most variability is seen between species, and these are the parts most interesting with respect to this review.

The function and design of joints in arthropods is rather interesting and will be briefly discussed here. Most of the different types of joints in arthropods function the same as different human joints, but their structure is much different, largely due to the fact that arthropods have an exoskeleton. Therefore, most of the 'joining' is accomplished on the outer parts of the body, rather than the inner parts.

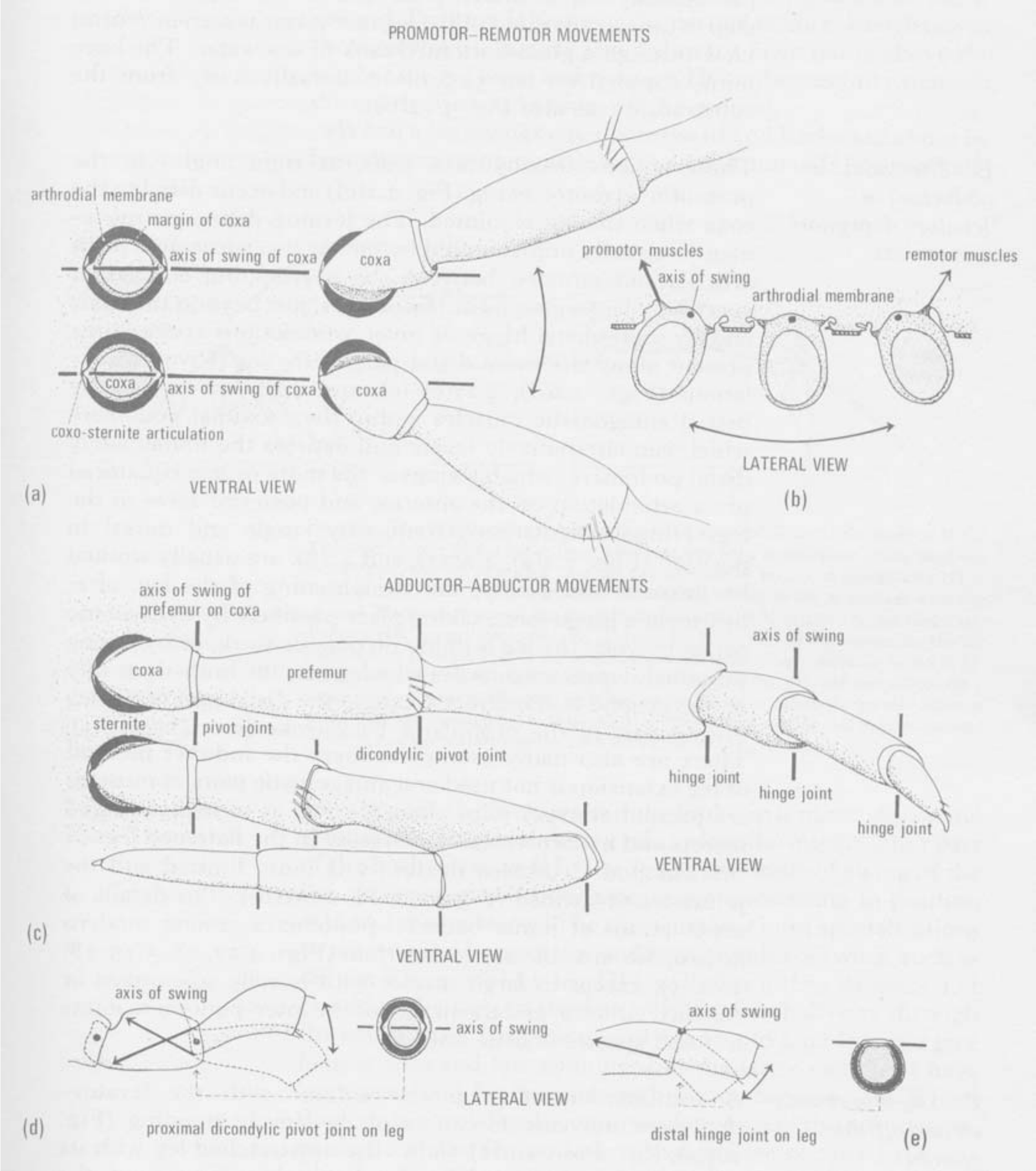


Figure 2: Joint analysis of a typical arthropod leg [Manton, 1977, p. 41]

Figure 2 shows the joint axes and type of movements of a typical arthropod limb. Note that all axes except the coxa are parallel to one another (parts (a) and (c)). This appears to be a rather peculiar result, but is actually quite similar to the arrangement of a human finger, hand, and forearm. Part (b) shows arrangement of the coxa, floating on the arthrodial membrane, and is not hinged by a stiff joint. The other joints are hinged by means of one or two condyles, which are socket-type joints. The links are held together by muscle (figure 3).

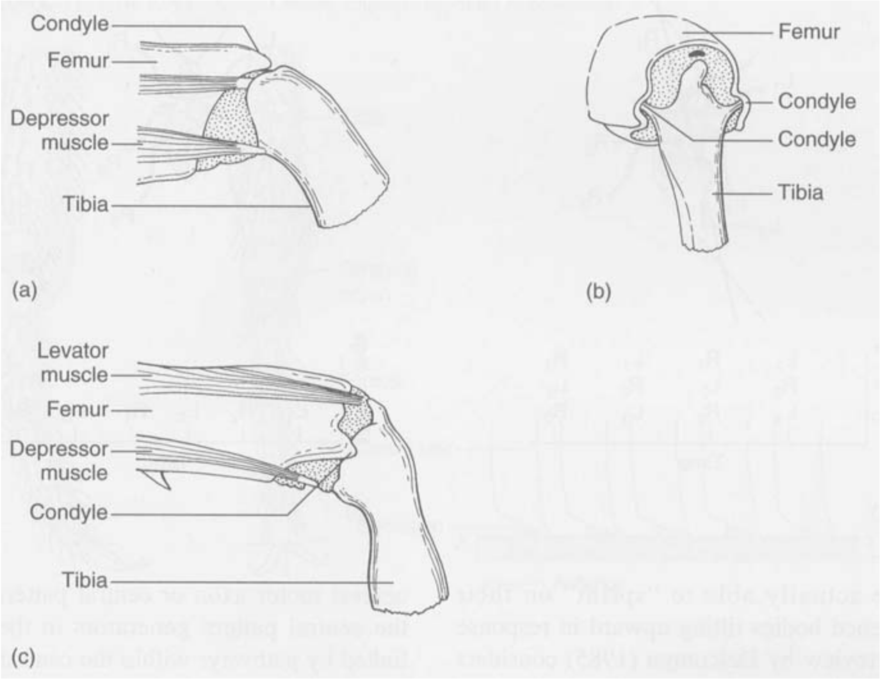


Figure 3: Two representative arthropod joints with one condyle (a) and two ((b) end view and (c) lateral view) [Romoser, Stoffolano, 1998, p. 209]

Some arthropod joints, particularly in crustacea, are arranged like hinges (figure 4). This arrangement is beneficial as it resists force in the direction of the limb and holds the links together. This also eliminates the need for muscles to hold the joint together.

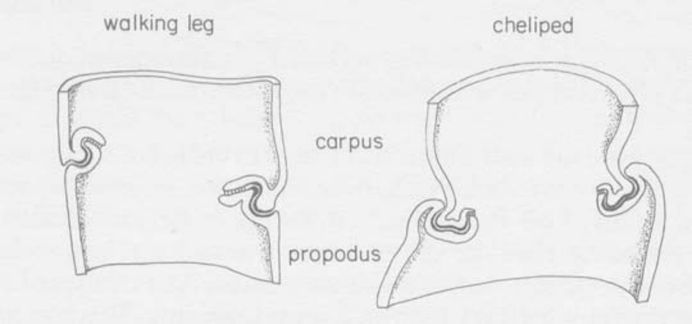


Figure 4: Hinge joints of crustacea for walking leg and cheliped [Warner, 1977, p. 30]

Particularly in between body segments, but many times in other joints, arthropods have a 'living hinge' joint that allows motion beteen the two links (figure 5). This hinge is primarily made of a rubber-like substance called resilin, and serves to seal the joint and sometimes provide useful elastic potential energy.

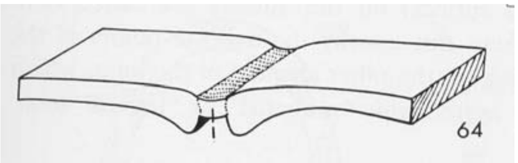


Figure 5: Chitin plates (exoskeleton) joined with a 'living hinge' [Nachtigall, 1974, p. 13]

The tarsus and pretarsus are the elements of the insect leg that have in some species evolved to the point where it can function as a gripper, such as a claw in crabs. In arthropods, these 'grippers' are primarily used for the capture of prey, and are sometimes used in combat. And although it seems natural for the far-most parts of the limb to be used for prey-capture, this is not always the case. The praying mantis and other ambush insects, for instance, uses the tibia and femur, equipped with specialized spikes, to capture their prey (figures 6, 7, 8).

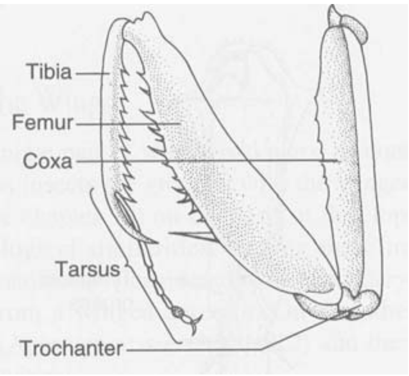


Figure 6: Morphology of the praying mantis forelimb [Romoser, Stoffolano, 1998, p.41]

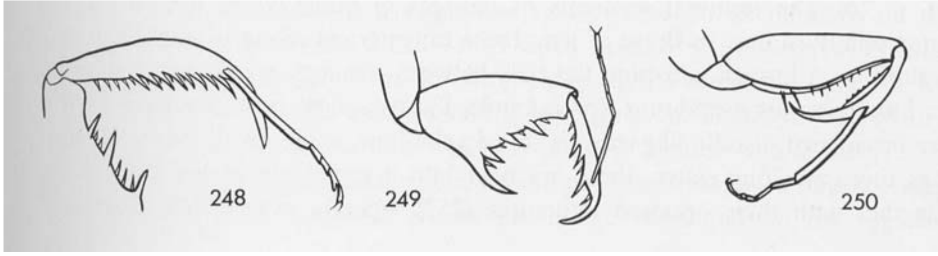


Figure 7: Forelimb design of other mantids [Nachtigall, 1974, p. 57]

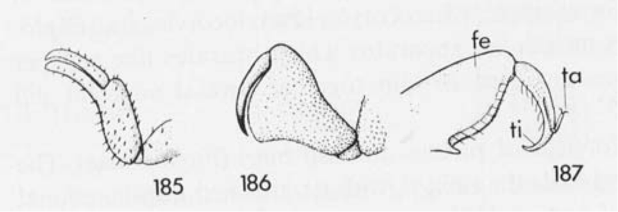


Figure 8: Forelimbs of various ambush bugs [Nachtigall, 1974, p. 48]

A number of male beetles have huge (in comparison to their body size) claws at the front of their bodies used for combat with other male beetles (figure 9). These, too, are simply legs that have evolved to serve a function other than walking.

Figure 9: A beetle with huge, claw-like mandibles [Nachtigall, 1974, p. 55]

Most prevalent in the literature are studies on the function and structure of crustacean claws, particularly crabs and lobsters. There are a number of reasons for this, but it is mostly due to their size and availability. [Warner, 1977]

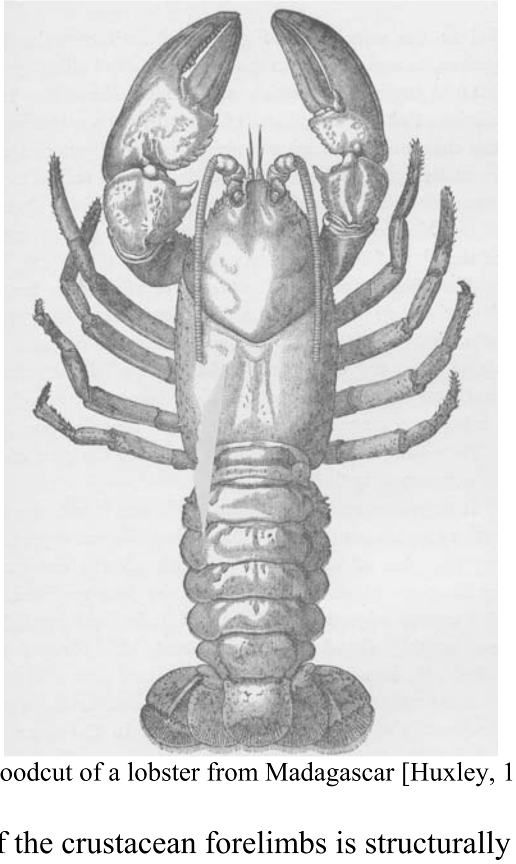


Figure 10: Woodcut of a lobster from Madagascar [Huxley, 1896, p. 251]

The physiology of the crustacean forelimbs is structurally similar to the generalized insect leg discussed above, but have been named differently (figures 11 and 12). The claws are referred to as the chela or chelipeds, and comprise of the propodus and the dactylus. Generally, each claw serves a different functional purpose and are therefore structurally different, details of which will be discussed later.

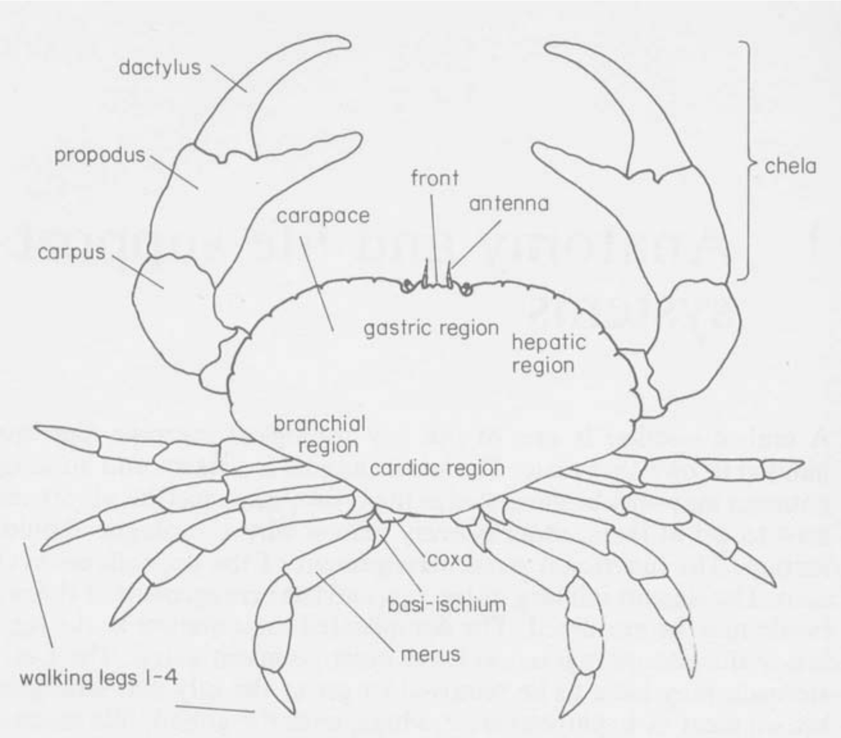


Figure 11: External parts of a European edible crab [Warner, 1977, p. 2]

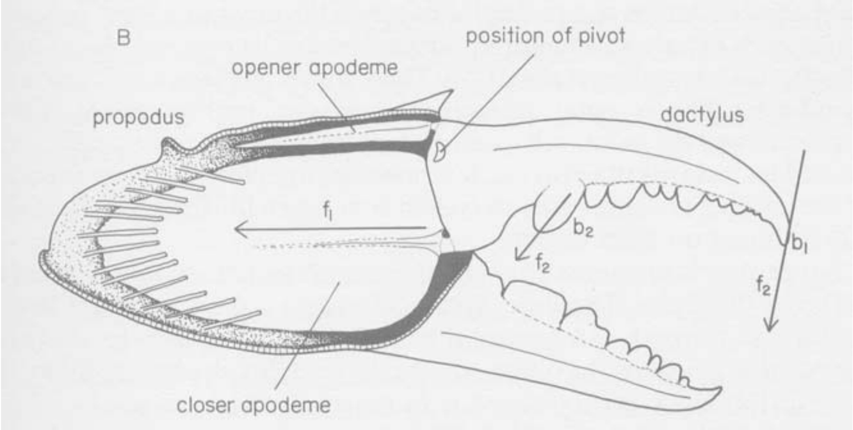


Figure 12: Internal parts of a crab cheliped showing force vectors [Warner, 1977, p. 27]

As with most body parts on most organisms, the claws of different species of crustacea have been specialized to perform certain tasks specific to that species' lifestyle. Figure 13 below shows the claw structure for a number of different species. The claw dipicted in A is for difficult crushing tasks; B for fast cutting; C for chipping mollusk shells; D for scraping algae from rocks; E for snatching at swimming prey [Warner p.88]. It is amazing to see how appropriate each design is for its specific task.

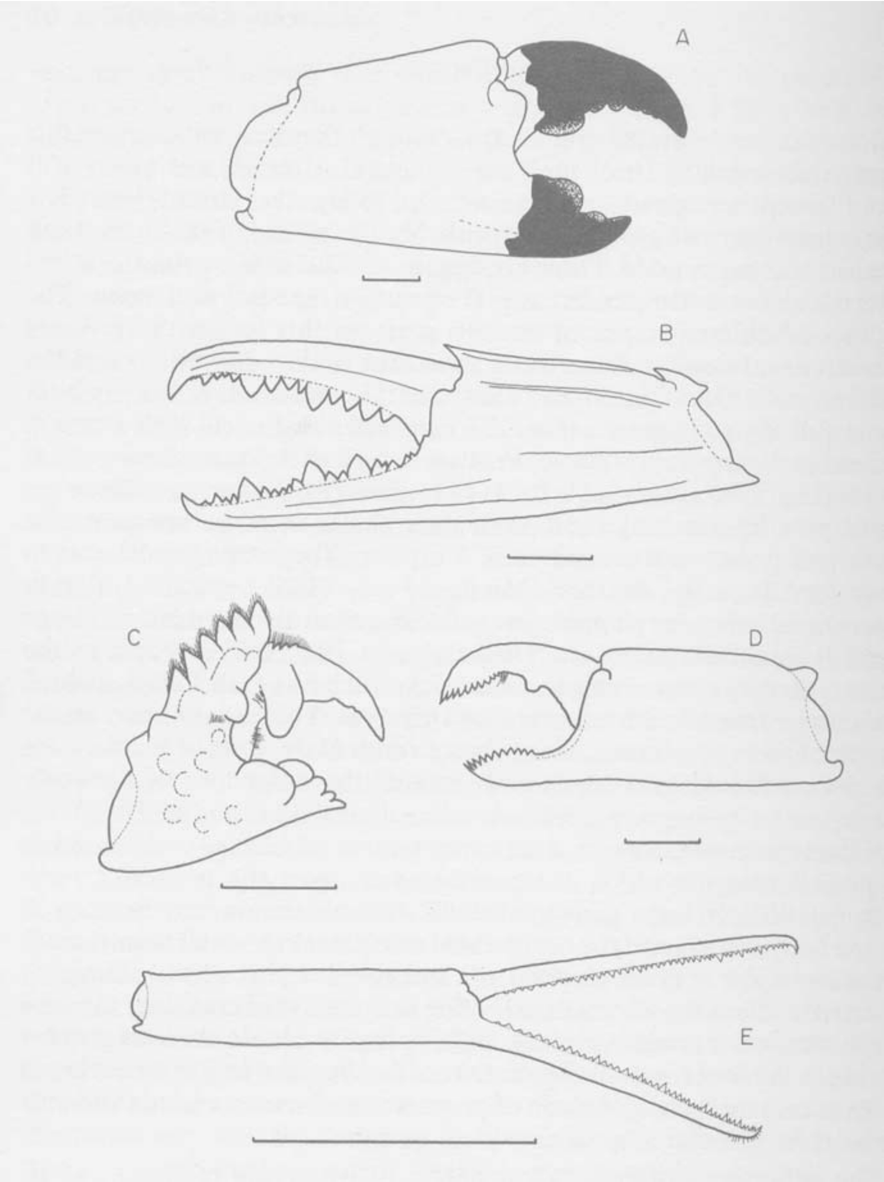


Figure 13: Claw structure for various crab species [Warner, 1977, p. 88]

Survey of Published Studies

In searching for literature on the topic of 'Arthropod Grasping and Manipulation,' very little was found at first, as was expected. It seems as though entomologists and biologists are more interested in naming, classifying, and observing than they are at analyzing and evaluating. This is not surprising, as we cannot expect biologists to think like engineers. However, a small amount of literature was found on the 'functional morphology' of the feeding appendages of crabs (decapoda: including lobsters) and also that of praying mantises. An overview of the literature on these two main topics will be presented here, followed by comments on applicable reports about other species that have been sprinkled throughout the literature.

Decapods

The claws of a crab have two main uses: combat and feeding. The first of these is less prevalent than the last, but is still significant and even interesting (especially to biologists). Combat can be seen as a social use of the cheliped. The literature on combat is fairly rich, and will be only briefly discussed here.

Hyatt and Salmon [1977] give a thorough analysis of combat in fiddler *crabs (uca pugilator* and *uca pugnax*). In these two species, males possess an enlarged claw which can be up to a third of their body weight! Females, although having a smaller claw, have many more chemoreceptors in their claws than males [Weissburg et al., 1996]. The male's enlarged claw can be used to signal females (figure 14) [Pope, 2000] and to fight with other males who are threatening to take over an owner's burrow. A complete analysis of typical fight sequences is given and analyzed. The authors do not report on the role of the claw (if any) in feeding.

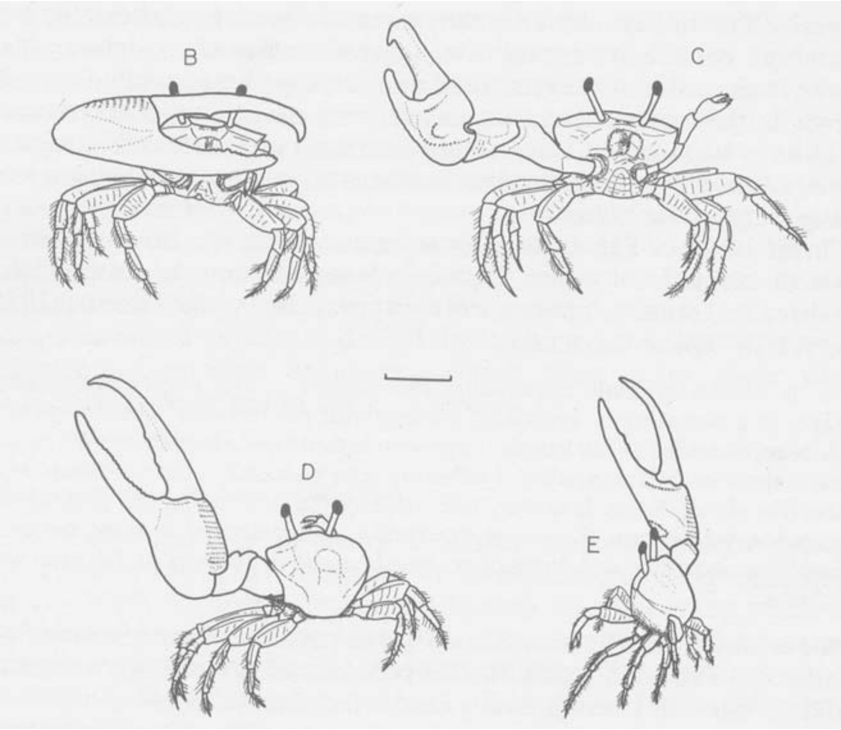


Figure 14: Claw waving sequence for a fiddler crab [Warner, 1977, p. 108]

In a paper addressing the role of proprioception in claw use, Hartman et al. [1997] present a classification of crab claw usage during feeding that could prove useful in future experimental or observational studies (table 2). The classification also sheds light on the many different ways that the crab claw is used during feeding.

Behavior	Description
Grip	Holding the valve between the dactyl and the pollex
Scrape	Using the dactyl to loosen meat from the valve
Grasp	Holding meat between the dactyl on pollex
Pull	Grasped meat is pulled from the valve
Carry	Chela brings loose meat to the mouth
Cut	Chela severs strands of meat held in the mouth from valve
Cradle	One or both chelipeds hold the meat to the mouth
Stabilize	One or both walking legs support or manipulate valve
Chisel	Pollex used as a wedge to loosen meat from valve
Guide	Chela used to push meat that is not grasped to mouth

Table 2: Classification and description of claw use during feeding on a mussel [Hartman et al., 1997]

The first six behaviors rely on the dactyl (grip - cut), while the last four (cradle - guide) are performed independent of the dactyl (see figures 11 and 12). The authors found that, when severing the afferent nervous signals from the chordotonal organ (proprioception for the dactyl muscle), the use of the dactyl was nearly eliminated, even though it was still functionally the same. This demonstrates the dependence of afference in the claw manipulation strategies of the crab.

Interestingly, the feeding behavior of decapods is largely driven by chemoreception in the location of food sources, rather than mechanoreception or vision. These chemoreceptors, somewhat like a nose in humans, are located on almost every part of the body of crustaceans, including the feet and even the general body surface (like having a nose in our armpit). In locating a meal, a decapod can walk along the ocean floor, 'smelling' the ground in search for food. Once a food source has been located (literally walked over), the decapod uses its legs to bring it to the front of the body, and then proceeds to eat it (by directing it to the mouth) or, if it is a shellfish, separate the meat from the valve. As a side note, the external mechanoreception in decapods and most other arthropods is done by hair-like sensillia protruding from gaps in the chitin of the exoskeleton (figure 15). [Derby, Atema, 1982]

Figure 15: Example of the hair-like sensillia in arthropods (taken using SEM) [Clarke, 1973, p. 28]

As was mentioned earlier, each of the two claws in decapods tends to serve a different functional purpose, and therefore tends to be structurally different from the other. Elner and Campbell [1981] present a nice analysis of the mechanical design and properties of the claws of the American lobster (*Homarus americanus*), focusing on each of the two chelae separately (figures 16 and 17). Members of this species possess the largest chelae of any crustacean; one specimen caught in Cape Cod weighed 17 kg and had a crusher chelae 39.5 cm in length and 48.3 cm in girth! The authors sought to analyze the mechanical advantage and force capabilities of the chelae of this species, using *in vivo* and *in vitro* measurement techniques.

The two claws are classified as 'cutter' and 'crusher' after the function of each, although the cutter chela is mostly used to hold the prey being squeezed by the crusher chela. The authors observed a maximum force of 256 Newtons produced by a single crusher chelae. As expected, it was observed that the crusher chelae could produce significantly larger forces than the cutter chelae, appropriate for their function. The resultant force produced by the chelae acts through the near middle of the dactyl biting edge. The mean mechanical advantages observed for the chelae were 0.33 for the crusher and 0.16 for the cutter. Male and female specimens did not differ significantly in this respect. The authors present plots of the force to length relationships in each of the chelae and present curve fits to the data (ln (N)=1.25 +.737 ln(mm) (R=.914, N=14) for crusher and ln (N)=.436+.866 ln(mm) (R=.944, N=11) for cutter). Although the authors present natural log fits to the data, they give no justification for this choice and a straight line fit seems just as appropriate (and simpler) by looking at the data.

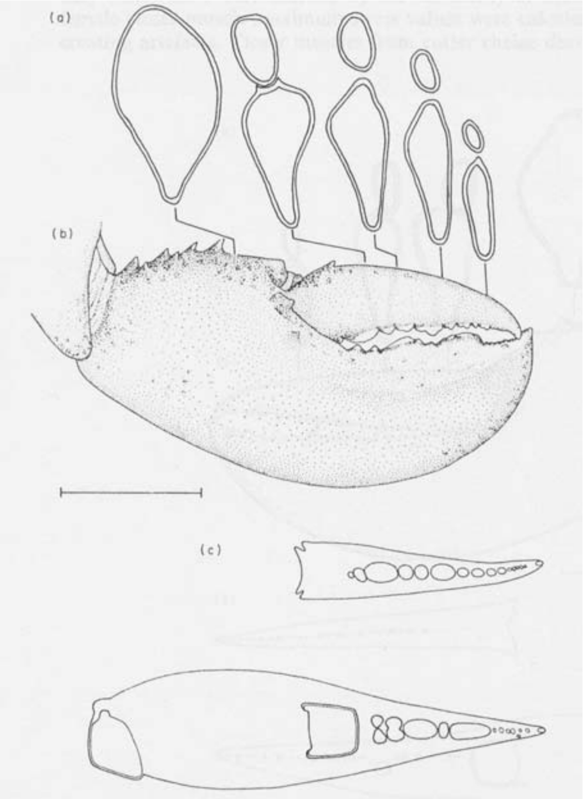


Figure 16: Crusher claw of the American lobster with cross-sections [Elner, Campbell, 1981, p. 277]

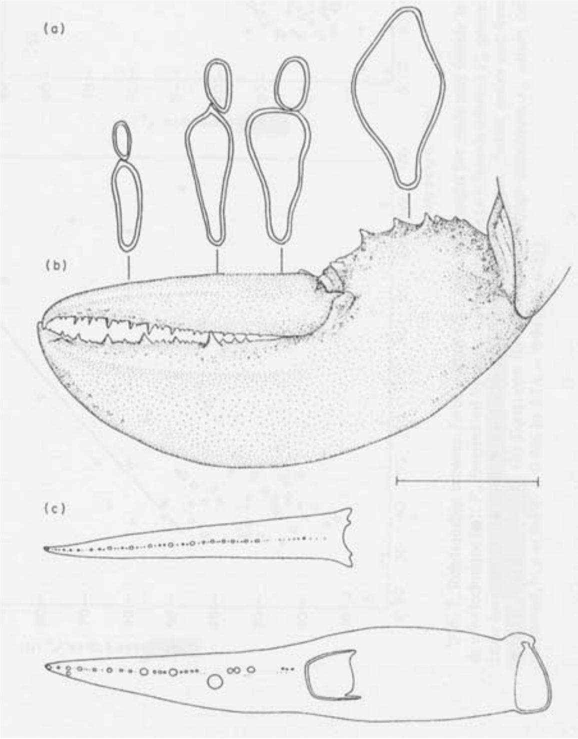


Figure 16: Cutter claw of the American lobster with cross-sections [Elner, Campbell, 1981, p. 278]

Mantids

Considerable focus has been given to the feeding and prey-capture behavior of the praying mantis. A significant reason for this is the ease with which a mantis can be provoked to strike, even when it is restrained. [Loxton, Nicholls, 1979]

In their paper "The functional morphology of the praying mantis forelimb," Loxton and Nicholls [1979] discussed the role of the design of the mantis forelimb, particularly that of the spines (figure 17) related to the capture of prey. Interestingly, some of the spines on the femur are hinged, bendable in only one plane, and the direction of movement is shown in figure 17 (B). The hinge is due to the arrangement of a stiff cuticle opposing a deformable cuticle (figure 17 (C)). (See the discussion on resilin presented later in this paper.) The cuticle stores elastic potential energy so that when the spine is released, it springs back to the extended position. The role of the spines (both stiff and hinged) was investigated in the way typical of anatomical investigations – they were cut off and the effect was observed.

It had been hypothesized that the spines served two main purposes: to impale the prey and to fill in the gaps between the femur and tibia to prevent escape (see figure 6). Indeed, the authors found that capture efficiency was reduced significantly as spines were removed and gave evidence in support of the above hypothesis. The hinged spines seem to serve as sensors (much like the mechanoreceptors described earlier and shown in figure 15), so that when prey has been captured the mantis will maintain tibial-femoral flexure.

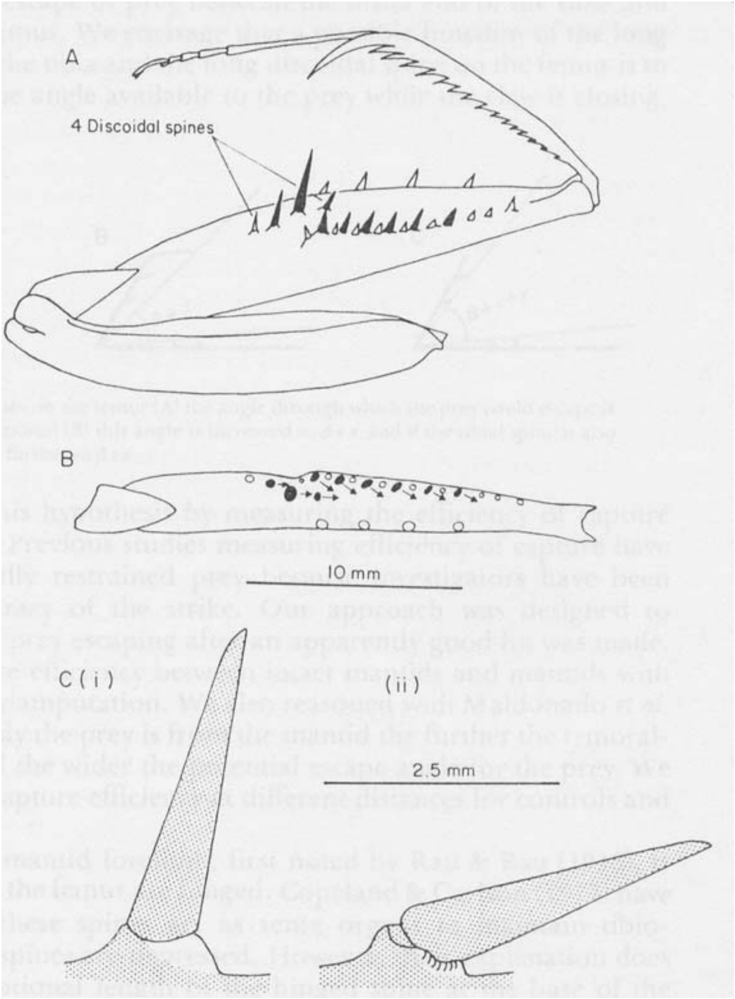


Figure 17: Forelimb of the praying mantis showing spine location and hinging properties [Loxton, Nicholls, 1979, p.186]

The authors went so far as to calculate the optimum prey radius based on the structure of the forelimb. The equation is given as:

$$r = T\frac{\sin(\beta - \alpha)}{2}$$

Where T=length of the tibia, α is the tibial-hook angle (figure 18) and β can be found iteratively by:

$$\tan(\beta - \alpha) = 2\frac{\tan\beta}{2}$$

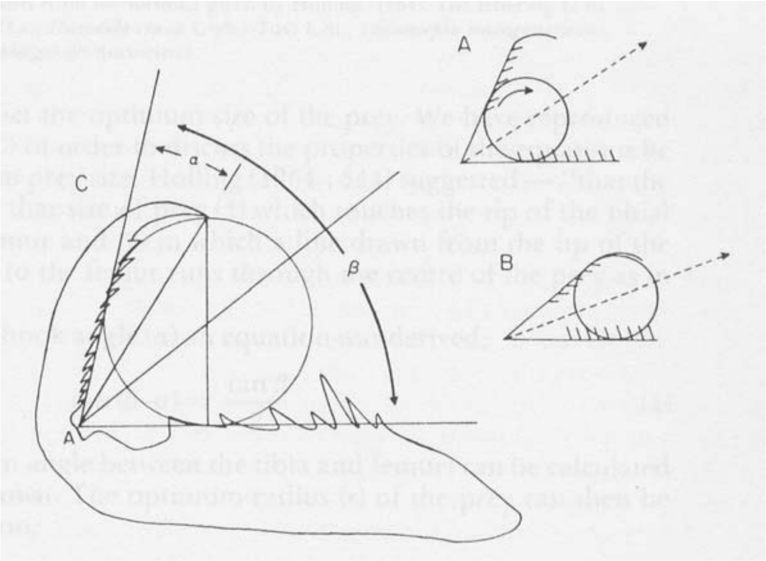


Figure 18: Angle assignment scheme showing α as the 'tibial-hook' angle [Loxton, Nicholls, 1979, p. 200.]

Corrette [1990] presents a nice analysis of the typical prey capture sequence of the mantis, paying particular attention to the joint angles throughout the motion. Figure 19 shows the classification scheme used for the joint angles and figure 20 gives a plot of these angles throughout the motion sequence.

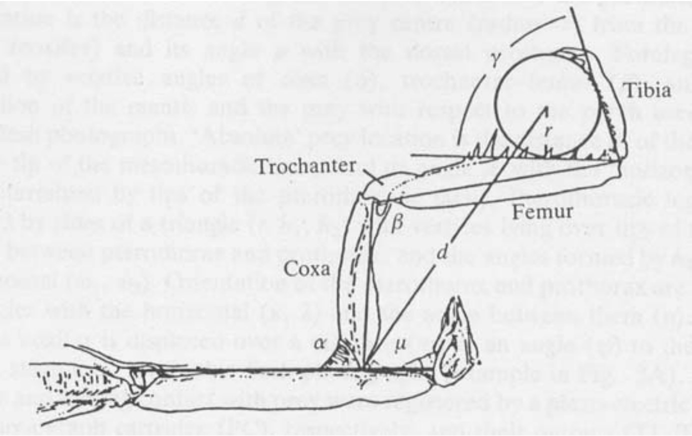


Figure 19: Diagram of the Praying mantis forelimb showing assigned joint angles [Corrette, 1990, p. 150]

Prete and Cleal [1996] investigated the body posture of the mantis for striking prey in different locations with respect to the mantis. The authors found two main postures for strikes in the mid-sagittal plane that they termed 'high' and 'low' strikes (figure 21). High strike position was used when the prey was 35° or more above the ground surface, and low strikes for those below this value. The authors also suggest that the mantis uses a combination of visual and proprioceptive information in coordinating the strike pattern for each individual case.

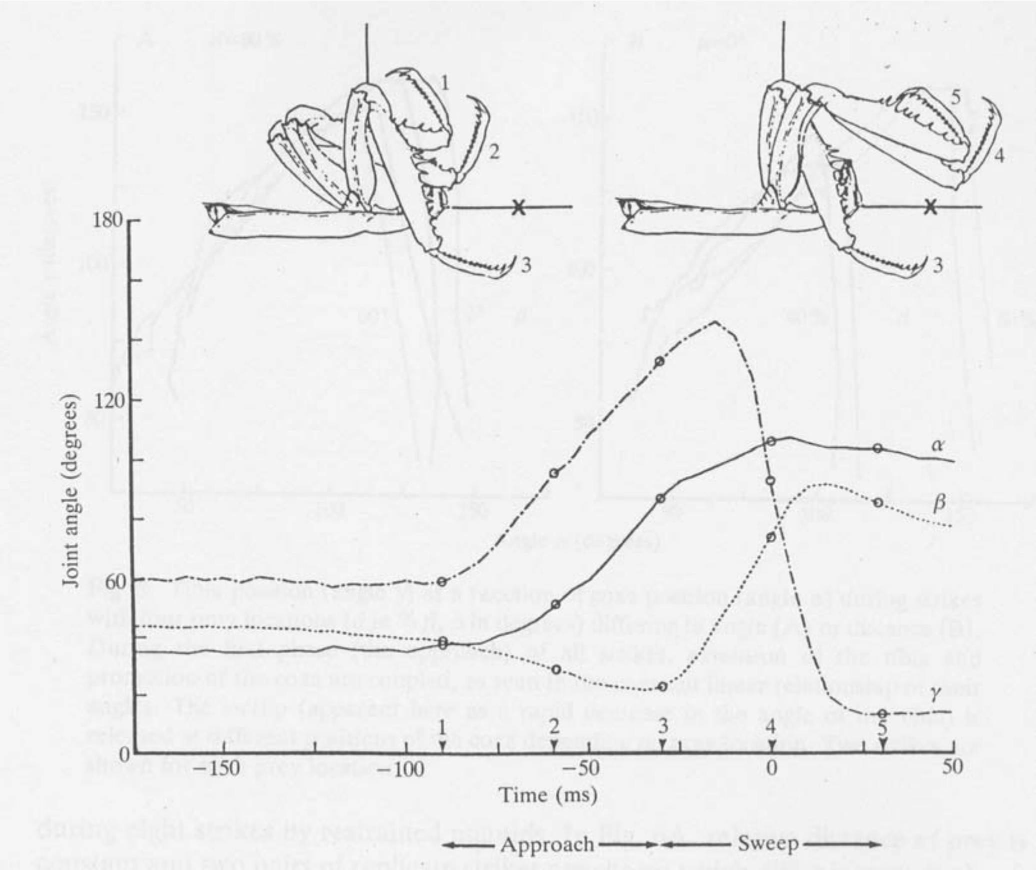


Figure 20: Plot of joint angles with respect to the phase in the capture sequence (see figure 19) [Corrette, 1990, p. 165]

In the horizontal plane, strikes did not fit into neat categories, but provided further clues about the coordination of the strikes (figure 22). Surprisingly, it was found that the movement of the mantis limbs closely resembled the escape turn motions of a cockroach (figure 22). These findings served to dispel many of the previously held beliefs that the mantis strike patterns were the result of specialized neuroanatomy that was unlike that of any other insect. The authors also found that the localization of prey is with respect to “pterothorax-centered space” rather than the previously held idea of being with respect to “head-centered space.”

Miscellaneous Findings

As was mentioned earlier, a number of articles have been recognized and reviewed that do not fall neatly into a group with one another, or their relevance in the scope of this review is questionable. However, those articles will be touched upon briefly here for the purposes of being thorough and to facilitate future investigations in this area.

Of great importance to the study of arthropod locomotion, and somewhat to grasping, is the discovery of the protein *resilin* in arthropod joints. Andersen and Weis-Fogh [1965] published a 65 page long article in a journal identifying the protein, giving its chemical and mechanical properties, and discussing its possible role in the insect cuticle. The protein was found to be much like the common polymer *elastin*, present in

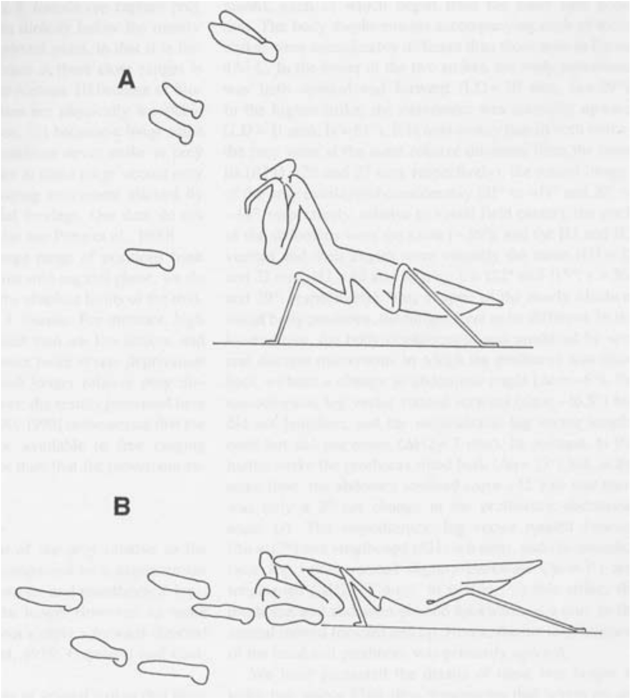


Figure 21: Praying mantis body position for the two different strike postions: high (A) and low (B) [Prete, Cleal, 1996, p. 179]

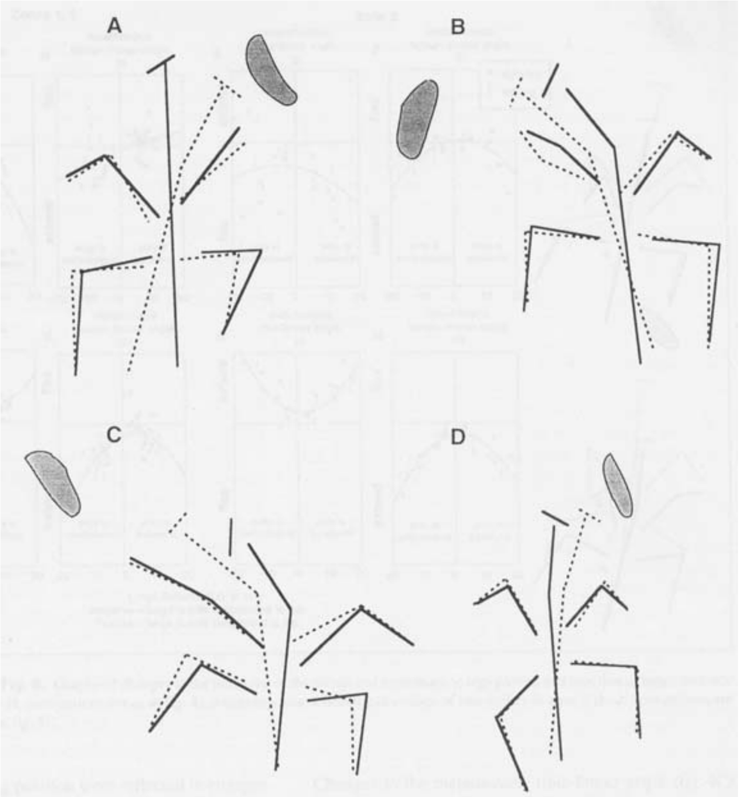


Figure 22: Praying mantis strike positions for varying prey locations in the horizontal plane. Solid lines = start position, dashed lines = position at time of strike, grey spot = prey loaction. [Prete, Cleal, 1996, p. 199]

many vertebrates. The two proteins are very rubber-like, and provide an amazing means of storing elastic potential energy. The authors identified it as the means with which locust wings are able to recoil.

Govindarajan and Rajulu [1974] identified the protein in the scorpion as the means with which the scorpion can open its chela, despite a lack of extensor muscles. Frazier et al. [1999] describe the role of elastic recoil in the tarsus of the cockroach during walking, also despite extensor muscles. Gorb [1996] describes the design of the insect unguitractor apparatus that serves to 'lock' the loaded spring in the insect tarsus. When desired, the spring is released, and the foot moves at a surprisingly rapid pace. This phenomenon has amazed many entomologists and is simply explained by the passive recoil due to the stored energy in the resilin molecules.

A number of papers (and one book – [Nachtigall, 1974]) were found that discuss the attachment mechanisms of arthropods to substrates. Many of these discuss the role of viscous fluids utilized by insects such as flies to walk up vertical substrates. Hasenfuss [1999] reports the role of this viscous fluid in combination with mechanical devices (figure 23) in the attachment strategies of certain caterpillars.

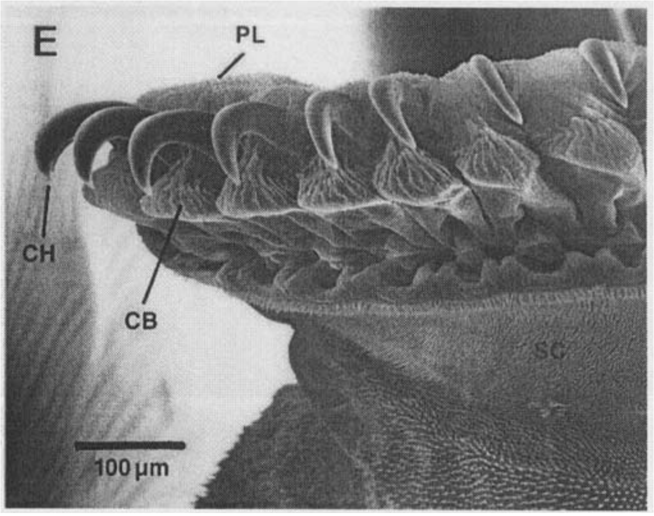


Figure 23: SEM view of caterpillar foot [Hasenfuss, 1999, p. 145]

In an intersting article, Gorb et al. [2000] describe the attachment pads of the great green bush cricket (*Tettigonia viridissima*). It was found that these pads are much like the soft, deformable human fingerpad, and grip the microstructure of substrates by deforming around them (figure 24).

A few papers were found that discuss the functional morphology of forelegs of other species that differ from those discussed in decapoda and the mantids. Felgenhauer and Abele [1983] discuss the ultrastructure of the feeding appendages of fresh-water shimp, focusing on the hundreds of tiny hairs, or setae, on each leg. These hairs serve as mechanoreceptors, scrapers for cleaning and feeding, and filters for feeding.

Gorb [1995] describes the predatory legs of three species of water bugs, comparing and contrasting between them. He places an empasis on the internal anatomy of the legs, and the way that the leg function differs because of this.

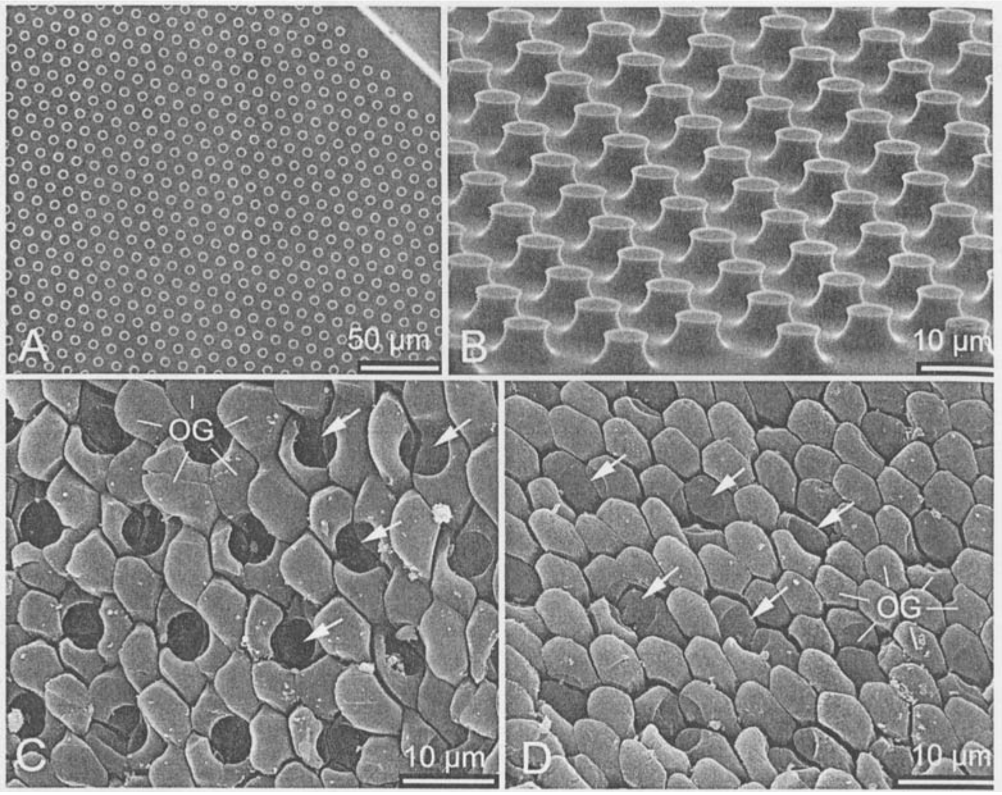


Figure 24: SEM views of Silicon substrate (A and B) and the attachment pads of the great green bush cricket when standing on the substrate (under strong load (C) and light load (D) [Gorb et al., 2000, p. 826]

References

S. A. Andersen, T. Weis-Fogh, "Resilin: A Rubberlike Protein in Arthropod Cuticle," *Advances in Insect Physiology*, volume 2, pp. 1-65, 1965.

Kenneth U. Clarke, *The Biology of the Arthropoda*, American Elsevier Publishing Company: New York, 1973.

B. J. Corrette, "Prey Capture in the Praying Mantis *Tenodera Aridifolia Sinensis*: Coordination of the Capture Sequence and Strike Movements," Journal of Experimental Biology, volume 148, pp. 147-180, 1990.

C. D. Derby, J. Atema, "The Function of Chemo- and Mechanoreceptors in Lobster (*Homarus Americanus*) Feeding Behavior," *Journal of Experimental Biology*, volume 98, pp. 317-327, 1982.

R. W. Elner, A. Campbell, "Force, Function and Mechanical Advantage in the Chalae of the American Lobster *Homarus americanus* (Decapoda: Crustacea)," *Journal of Zoology*, volume 193, pp. 269-286, 1981.

B. E. Felgenhauer, L. G. Abele, "Ultrastructure and Functional Morphology of Feeding and Associated Appendages in the Tropical Fresh-Water Shrimp *Atya Innocous* (Herbst) with Notes on its Ecology," *Journal of Crustacean Biology*, volume 3(3), pp. 336-363, 1983.

S. F. Frazier, G. S. Larsen, D. Neff, et al., "Elasticity and Movements of the Cockroach Tarsus in Walking," Journal of Comparative Physiology, volume 185, pp. 157-172, 1999.

Stanislav Gorb, "Design of the Predatory Legs of Water Bugs (Hemiptera: Nepidae, Naucoridae, Notonectidae, Gerridae)," *Journal of Morphology*, volume 223, pp. 289-302, 1995.

Stanislav Gorb, “Design of Insect Unguitractor Apparatus,” *Journal of Morphology*, volume 230, pp. 219-230, 1996.

S. Gorb, Y. Jiao, M. Scherge, “Ultrastructural Architecture and Mechanical Properties of Attachment Pads in *Tettigonia Viridissima* (Orthoptera Tettigoniidae*),” Journal of Comparative Physiology*, volume 186, pp. 821-831, 2000.

S. Govindarajan, G.S. Rajulu, “Presence of Resilin in a Scorpion *Palamnaeu swammerdami* and its Role in the Food-Capturing and Sound-Producing Mechanisms,” *Experientia*, volume 30, pp. 908,909, 1974.

P.J. Gullan, P.S. Cranston, *The Insects: An Outline of Entomology*, Blackwell Science: Oxford, 2000.

H. B. Hartman, E. E. Johnson, P. D. Storer, “Manipulation by the Crab Claw is Dependent Upon Chordotonal Organ Afference,” Journal of Experimental Zoology, volume 279, pp. 579-586, 1997.

I. Hasenfuss, “Adhesive Devices in Larvae of Lepidoptera (Insecta, Pterygota),” Zoomorphology, volume 119, pp. 143-162, 1999.

T. H. Huxley, *The Crayfish – An Introduction to the Study of Zoology*, Kegan Paul, Trench, Trubner: London, 1896.

G. W. Hyatt, M. Salmon, “Combat in the Fiddler Crabs *Uca Pugilator* and *Uca Pugnax*: A Quantitative Analysis,” *Behaviour*, volume 65, pp. 182-211, 1977.

G. S. Larsen, S. F. Frazier, S. N. Zill, “The Tarso-Pretarsal Chordotonal Organ as an Element in Cockroach Walking,” *Journal of Comparative Physiology*, volume 180, pp. 683-700, 1997.

R. G. Loxton, I. Nicholls, “The Functional Morphology of the Praying Mantis Forelimb (Dictyoptera: Mantodea),” *Zoology of the Linnean Society*, volume 66, pp. 185-203, June 1979.

S. M. Manton, *The Arthropoda: Habits, Functional Morphology, and Evolution*, Clarendon Press: Oxford, 1977.

Patsy A. McLaughlin, *Comparative Morphology of Recent Crustacea*, W.H. Freeman and Company: San Francisco, 1980.

W. Nachtigall, *Biological Mechanisms of Attachments: The Comparative Morphology and Bioengineering of Organs for Linkage, Suction, and Adhesion*, Springer-Verlag: New York, 1974.

F. R. Prete, K. S. Cleal, “The Predatory Strike of Free Ranging Praying Mantises, Sphodromantis lineola (Burmeister). I: Strikes in the Mid-Sagittal Plane,” *Brain, Behavior, and Evolution*, volume 48, pp. 173-190, 1996.

F. R. Prete, K. S. Cleal, “The Predatory Strike of Free Ranging Praying Mantises, Sphodromantis lineola (Burmeister). II: Strikes in the Horizontal Plane,” *Brain, Behavior, and Evolution*, volume 48, pp. 191-204, 1996.

D. S. Pope, “Testing Function of Fiddler Crab Claw Waving by Manipulating Social Context,” *Behavior, Ecology, and Sociobiology*, volume 47, pp. 432-437, 2000.

William S. Romoser, John G. Stoffolano, Jr., *The Science of Entomology*, McGraw-Hill, Boston, 1998.

Frederick R. Schram, *Crustacea*, Oxford University Press: Oxford, 1986.

Gilbert Waldbauer, *The Handy Bug Answer Book*, Visible Ink Press: Detroit, MI, 1998.

G. F. Warner, *The Biology of Crabs*, Van Nostrad Reinhold Company: New York, 1977.

M. J. Weissburg, J. Pearce, C. K. Govind, C. D. Derby, “Sexually Dimorphic Patterns of Neural Organization in the Feeding Appendages of Fiddler Crabs*,” Cell & Tissue Research*, volume 286, pp. 155-166, 1996.