RESEARCH STATEMENT
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The fundamental animal behaviors of feeding, reproduction, locomotion, and defense require movement; indeed any behavior that allows an animal to physically interact with its environment bears the same requirement. This idea gives rise to my main academic interest: the analysis of joint structures and functions that allow movement in soft-bodied invertebrates. While the topic is broad, my point of departure is very basic: organisms move by translating or rotating one of their parts relative to the others. Therefore, the crucial mechanical element of moving structures is the flexible area that permits motion, or the joint. Thus, I seek to integrate morphology, comparative biomechanics, physiology, and neurobiology to characterize poorly understood soft tissue joint mechanisms. Additionally, joint characterizations not only help explain performance of critical animal behaviors, they often inform on broader questions such as the identification of general mechanical principles via comparative morphology, the relation of adaptive functional characteristics of a mechanism to its ecology, and the characterization of evolutionary trends by using morphological traits in phylogenetic analyses.

The history of animal joint analysis is ancient. As early as 350 BC, Aristotle identified the joint as the critical structural element that allowed motion in walking, flying and swimming appendages. However, until relatively recently, the primary focus of joint biomechanical studies have been on vertebrate and arthropod joints. Here, articulating surfaces of skeletal elements contact each other within the joint and muscles that span this area of contact generate forces for movement. This focus is not surprising since our own articulated joints represent a robust morphology that allows efficient force transmission across the joint and safe control of range of motion. However, there are organisms that possess joints without articulating surfaces yet still offer support to the rigid elements that they connect. In their simplest form, these flexible joints are represented by a thin area within a continuous rigid element at points where flexibility is required. This morphology is thought to have limited use, however, as it tends to buckle when loaded in compression. This is not the case in more complex forms of flexible joint. Here, the skeletal elements are connected together by intricate arrangements of flexible connective tissue and muscle fibers. Such joints are capable of a great complexity, diversity and range of motions, often along all three axes, yet do not buckle when forces are transferred from element to element. To describe this type of joint, I coined the term “muscle articulation” to describe its novel morphology and have since found it to be of critical use in a wide variety of unrelated soft bodied invertebrates.

**Summary of research on muscle articulations**

The following projects characterizing muscle articulations are based on data that have been collected as part of my doctoral dissertation with Dr. W.M. Kier at the University of North Carolina at Chapel Hill (UNC).

1. *Octopus morphology*

The joint associated with the beaks of *Octopus bimaculoides* was the first described muscle articulation. The upper and lower beaks are embedded in several sets of muscles such that they make no contact within the joint. Using gross dissections, sets of mutually perpendicular histological paraffin thin sections, and computer graphics reconstruction software, I described the three-dimensional arrangement of the muscle fibers within the beak muscles. From these analyses, I hypothesized a) that a robust closing muscle brought the upper and lower beaks together and b) that a putative opening muscle, by virtue of its multiple orientations of muscle fibers (known as a muscular hydrostat), opened the beaks, created the pivot mechanism, and bore the compressive bite reaction forces.

2. *Octopus functional mechanics*

Definitive tests of functional hypotheses followed the morphological description of the octopus buccal mass. Using *in vitro* preparations of this structure, I recorded muscle onset activity using fine-wire electromyography while recording the opening and closing positions of the beaks using a custom-made movement monitor circuit. The results of these techniques, supported by the morphological findings, seem to confirm the functioning of the octopus muscle articulation. The putative opening muscle was indeed found to be capable of, a) not only generating the force required to move the beaks with a great range of motion, but b) stabilizing the repositionable axis of rotation within the joint, and c) transmitting the compressive forces resulting from biting motions from one beak to the other without buckling. I presented these results at the 2005 meeting of the Society for Integrative and Comparative Biology (SICB) where it was awarded the Best Student Presentation award for the Division of Invertebrate Zoology.

3. *Polychaete worm jaw and flatworm hook morphology*

To gauge the importance of the muscle articulation, I wanted to test whether its mechanical principles were limited to the special case of the octopus beak joint or if these joints are more widely used in animal kingdom. Indeed, I have found a number of other muscle articulations and am currently assessing the diversity of their forms and functions. Specifically, the zinc-strengthened jaws embedded in the muscular eversible pharynx of the errant polychaete *Nereis virens* and the eversible proboscis hooks of an interstitial marine flatworm known as a Kalyptorhynch turbellarian seem to share all the biomechanical characteristics of the octopus buccal mass muscle articulation.

Jaws of *Nereis virens* are positioned on either side of the mouth and rely on hydrostatic mechanisms to open them. A morphological analysis of soft tissue fiber orientations suggests that they represent a complex muscular hydrostat with multiple functional areas that contract to antagonize each other in moving the jaws and form a hard area to support the joint pivot. This morphological description was first presented at the 2006 meeting of the SICB and was based on plastic semithin histological sections, as well as a new technique using radial microscopical computer tomography developed by me (hardware) and two collaborators (software) at the Department of Computer Science, UNC, Drs. M. Polleyfes and L. Vicci.

Analysis of the putative flatworm muscle articulation required collaboration with a meiofaunal systematist, Dr. M. Hooge, at the University of Maine. With the specimens of Kalyptorhynch flatworms that he has provided, I have used fluorescence immuno-labelled specimens to visualize the muscle fibers within these microscopic muscular proboscides using Confocal Laser Scanning and Differential Image Contrast microscopy techniques. Non-muscular soft tissues were analyzed using histological thin sections made from epoxy-embedded specimens. Here, I have identified a single orientation of muscle fibers that is associated with a tension bearing connective tissue antagonist, suggesting a novel form of muscle articulation that may not require multiple orientations of muscle fibers to resist compressive forces.

## Summary of other areas of research

1. *Underwater movement monitoring system*

An area of the scientific process that holds great interest for me lies in developing, inventing, and learning new techniques. An example of this is my collaboration with Dr. H. Hsiao of the UNC Department of Biomedical Engineering. We designed and built a two-electrode movement monitor that measures changes in underwater distances. I used this device to track the position of the octopus beaks during my functional testing experiments. As the value of discovery for me is intimately related to teaching this project was doubly rewarding as I have published the technique for use by others in the journal of Invertebrate Biology and with the help of data collected by my undergraduate student, Ms. M. Lee.

2. *The evolution of form and function of gastropod tarsic foot musculature*

This project is an offshoot of my master's research performed at the University of Calgary, AB, Canada with Dr. G. Bourne and illustrates my early and continuing interest in invertebrate systematics. Initial research performed by Dr. J. Voltzow, University of Scranton, PA, identified an evolutionary trend in the musculature of the gastropod foot (the tarsic muscles), from distinct and robust in primitive prosobranchs to quite integrated and slight in neogastropods. I described foot musculature characteristics for a larger number of snails within the "prosobranchia" as well as opisthobranchs and pulmonates. I also learned DNA sequencing techniques and sequenced the DNA encoding the16S Ribosomal RNA subunit. The morphological traits map quite closely to the molecular phylogeny and both suggest that the basal prosobranchs are polyphyletic. A number of rarer specimens remain to be examined and in this effort, I have received a Lerner-Grey Fellowship to support further research and have begun to collaborate with Dr. Voltzow to develop a more complete characterization of the subclass taxa within the Gastropods.

## Future Directions

I am working to more precisely define the biomechanical characteristics of muscle articulations by investigating the details of their structure and function that allow an unparalleled range of complex and diverse movements. In the future, I will continue to document the diversity of muscle articulation forms and functions as they appear in other soft-tissue mechanisms among the invertebrates. A small subset of these may include the valves of inarticulate brachiopods and chitons, and the larval mouth parts of tree burrowing insects. However, now that something is known of their form and function, perhaps the most important advances in the characterization of muscle articulations will be in their control. Where articulated joints have mechanical limits to range of motion, the soft tissues of muscle articulations may impose no such limits. Thus understanding the control of these flexible joints will be crucial in their analysis.

In a broad sense, the investigation of the form, function, and control of muscle articulations represent the foundation of a wider research program. Aspects of invertebrate joint analyses are important to many biomechanical, ecological, and evolutionary questions. Can we engineer practical, biologically-inspired artificial muscle articulations? As animals tend to use muscle articulations in the manipulation and consuming of food items, how do the biomechanics of these joints relate to an organism's feeding ecology? How do muscle articulations evolve and can the documentation of their evolutionary change provide valuable phylogenetic information? Why do they generally occur in soft-bodied organisms? I look forward to directing my research program towards many of these questions in the future.