I arranged the articles in a way that starts of describing the attachment behaviour of remoras which I transitioned it into the structure and the mechanisms of attachment, then into the evolutionary aspect of the adhesion disc, and lastly attempts at bio-inspired discs. I thought this was the best way to demonstrate the literature in this field because first by understanding the basics of the behaviour, it would make more sense and the reader would be able to relate the structure of the disc to the function more easily, which would also then help the reader understand the behaviour from an evolutionary standpoint.

Sazima, I., & Grossman, A. (2006). Turtle riders: Remoras on marine turtles in Southwest Atlantic. Neotropical Ichthyology, 4(1), 123–126. https://doi.org/10.1590/S1679- 62252006000100014

This article reviews the research that explores the “hitch-hiking” behaviour of remoras’ as they attach to marine turtles in the Southwest Atlantic. The specificity of host attachment varies based on the species of remoras, as some attach to one host whereas others can attach to multiple. This paper specifically explored the interactions between two species of remoras and four turtle species - they explored what species attach to marine turtles, the remora/turtle host ratios, the occurrence of this interaction in the Southwest Atlantic, and possible advantages/disadvantages for the host. The remora/turtle ratios were taken from two sites where the turtle numbers were known, and they showed that the higher the ratio was, the greater the hydrodynamic drag experienced by the host while swimming. This can be a disadvantage for the host when they have to escape from predators or when they compete for mating partners. The remoras on the other hand benefit as they conserve energy in locomotion, can be introduced to new mates attached on other turtles, and don’t need to forage for themselves. Two instances showed that the sharksucker remoras consume on particles by detaching from the host or remaining attached. This is affected by how much the host disturbed the substrate. The further the substrate falls, the more likely the remora is to detach. It was also pointed out that most of the recorded interactions were with juvenile remoras and the adult remoras were attached as couples, indicating they may be mating pairs. This relates to the remora/turtle ratio and drag as it would increase if the remoras are adults and attaching in pairs relative to juvenile remoras.

**Article Contribution:** This review article provides a detailed summary of the interaction of remoras and turtles in the Southwest Atlantic. Most articles I found on the topic don’t explore the interaction between a specific host species and remoras. It also provides an insight to how the remoras feed on the substrates that are disturbed by the host, and the specific places they attach to. However, since this paper was based solely on the poorly documented interactions in Southern Atlantic, future research can be conducted in other areas. Additionally, interactions between remoras and different species instead of turtles can be explored.

Flammang, B. E., Marras, S., Anderson, E. J., Lehmkuhl, O., Mukherjee, A., Cade, D. E., Beckert, M., Nadler, J. H., Houzeaux, G., Vázquez, M., Amplo, H. E., Calambokidis, J., Friedlaender, A. S., & Goldbogen, J. A. (2020). Remoras pick where they stick on blue whales. *Journal of Experimental Biology*, *223*(20). <https://doi.org/10.1242/jeb.226654>

Although the symbiotic relationship between remoras and marine animals is known, the reason for remoras selecting specific locations on certain animals is not well understood. It’s been assumed that they adhere to locations where drag is minimized, areas where the host would be less irritated, or where there is more likely to be food; however, there is not enough evidence to justify these claims. Therefore, the authors try and discern any clear pattern or where the remoras stick, and why they choose those areas. They analyzed video recordings of blue whales in the ocean and performed empirical and computational fluid dynamic analyses. Through the development of biological tags, the position of remoras was easier to be studied. The authors were able to obtain video footage of remoras from these multi-sensor video bio-logging tags, from which further computational analysis can occur. Furthermore, to test for site specificity, a Rayleigh distribution test for non-uniformity was used.

The remoras were observed behind the blowhole, next to/behind the dorsal fin, above/behind the pectoral fin, and remoras were seen to cluster in some of these regions. Remoras would remain attached to these locations during whale surfacing too, so they’d be exposed to the air for some time. Furthermore, no remoras were seen on the ventral surface, and Rayleigh’s test for non-uniform distribution further confirmed that remoras attach to specific sites and in clusters. Remoras were also able to move around to get food, so they were not stationary the entire time. The authors were able to deduce that remoras prefer regions where there is low drag, and even though there were remoras in areas that experienced high drag, there was never a cluster there. Furthermore, since the remoras are not attached to the ventral side, this may be to avoid predation from sea birds.

**Article Contribution:** The reason I chose this paper was because they were able to provide evidence and support for why remoras chose areas where drag was reduced, which previously was not fully justifiable. Prior to the tagging method used in this study, there were only single photographs which is not enough to prove why they were in certain areas, so having video evidence makes the claim much more plausible. Areas of future research can be seeing whether they choose similar areas in sharks where drag would be minimized to further confirm their findings.

Cohen, K. E., Flammang, B. E., Crawford, C. H., & Hernandez, L. P. (2020). Knowing when to stick: Touch receptors found in the remora adhesive disc. Royal Society Open Science, 7(1), 190990. https://doi.org/10.1098/rsos.190990

The article focusses on understanding the mechanism behind remoras’ ability to sense their environment, which permits them to attach to larger marine animals to form a symbiotic interaction. The “hitch-hiking” behaviour increases locomotive efficiency for the remoras, while also benefiting the hosts as the remoras consume on parasites. The main focus of this paper is on a pushrod mechanoreceptor complex which was found in a previous study; however, no function was attributed to this structure in that study. The authors therefore shifted their attention to the morphology of this structure in order to try and understand how it helps in their sensing capabilities.

*Echeneis* *naucrates* were used as sample organisms as they can bind to many different host types, meaning they would be most representative of other remoras. In order to observe the morphology, they removed the head and disc of the remoras and used microtomographic scanning to measure the abundance of push-rod mechanoreceptor complexes in the anterior and posterior regions of the discs. Furthermore, scanning electron microscopy was performed on sections of the anterior, middle and posterior lip to see if there were receptors on the lamellae (structures responsible for adhesion). They also studied the discs of all known remora species using a dissecting microscope to quantify the abundance of mechanoreceptors along the disc. The study shows that the mechanoreceptors complexes were primarily found anteriorly for all remora species no matter what their habitat or host species is. These complexes were also not grouped together, rather scattered along the entire disc. This discovery suggests that increased sensitivity to mechanical stimuli on the anterior end is necessary for the function of the adhesive disc. Further research can be done to see whether this Is because either attachment is initiated anteriorly or because adhesion loss initiation begins at the anterior portion.

**Article Contribution**: I chose this article because of the lack of research regarding the sensory abilities of remoras. Most articles I found were regarding the mechanism of attachment, and not the push-rod mechanoreceptor complex discussed in this study. These mechanoreceptors were found for the first time in fishes and are normally not that prominent in vertebrates either. This paper has opened up many new areas of research that can deepen the understanding of the behavior, for example, trying to see why these mechanoreceptors are more abundant in the anterior portion of the dorsal lip of the adhesion disc.

Beckert, M., Flammang, B. E., & Nadler, J. H. (2015). Remora attachment is enhanced by spinule friction. *Journal of Experimental Biology*, jeb.123893.

<https://doi.org/10.1242/jeb.123893>

Remoras attach to marine animals through dorsal suction pads which are made of pectinated lamellae that are homologous to dorsal fin elements. Lamellae have projections called spinules, which are assumed to increase resistance to slippage, and thus help a remora stick-on hosts. The study focusses on the underlying mechanisms behind the attachment function of remoras and a numerical analysis of forces that come into play with the behavior. The contact surface topology was measured by its radially averaged power spectrum, C(w), which was measured using an LEXT OLS4000 3D material confocal microscope. The frequency and amplitude components of shark skin were obtained from a Shortfin mako using confocal microscope data. Shortfin mako were chosen as the sample species because they are readily available and are fresh specimen. Furthermore, individual spinules and tip locations were identified by using Rhinoceros 3D. Friction coefficient is the ratio of friction and normal forces, and they are measured for natural and artificial spinules on glass substrates that had known topologies.

Friction coefficients obtained from real remora spinules was similar to that of artificial spinules on glass substrates. There are a high number of engaged spinules that increase the friction on rough surfaces, which help the remoras remain attached to fast-moving hosts. Furthermore, the tip shape was found to determine the minimum spatial frequency (wavelength) that the spinule can access of a surface, where maximum friction was observed when there was minimum frequency. At long wavelengths (hosts with smooth skin), sharp tips and the actual tips could both enter surface valleys so there is minimum frictional enhancement. Relative to shorter wavelengths (hosts with rough skin), only the sharper tips were able to enter surface valleys so these sharper tips can develop larger friction coefficients, and therefore are more effective in attaching to animals with rough skin.

**Article Contribution:** I chose this article because measuring the friction across multiple length scales is difficult on a biological system therefore, in order to understand the mechanics behind resistance, modeling the interfacial action is necessary, which this article tried to tackle. Furthermore, there has not been any experimental confirmation of the mechanisms behind the forces that relate to attachment. One future area of research in this field can be determining the effect of soft tissue from the remora pad, which was controlled in this experiment as it normally would start deforming when contacted by a rough surface.

Flammang, B. E., & Kenaley, C. P. (2017). Remora cranial vein morphology and its functional implications for attachment. *Scientific Reports*, *7*(1), 5914. <https://doi.org/10.1038/s41598-017-06429-z>

Remoras are able to resist high-shear conditions due to the function of the adhesive disc that evolved from the dorsal fin spines of fishes. The evolution of this complex structure required extensive reorganization of the skull and fin spines, but the role of the soft tissue in the adhesion disc is not well understood. Therefore, the authors wanted to explore the function of soft tissue in the adhesion properties of the disc, which have not been analyzed before.

Remoras were kept in aquaculture tanks where they were exposed to 12:12 hour light: dark cycles. Furthermore, the remoras were fed custom fish, shrimp, and vegetable mix daily. One remora was euthanized via a tricaine methane sulfonate overdose and dissected for an electromyography study, two remoras were used for imaging cranial vasculature after the fish were euthanized by a overdose of Tricaine-S. One remora was anaesthetized using Tricaine-S and injected with blue-food dye into the lamellar component of the suction disc. Lastly, one fresh, and one preserved cobia (*Rachycentron canadum)* was dissected so it could be compared with the remora.

The remora that was dissected showed large diameter blood vessels which were situated dorsally to the skull and was in contact with the ventral side of the lamellae and the musculature of the adhesive disc. These large cranial veins are between the pectinated lamellae of the disc and the dorsal aspect of the cranium, meaning that when lamellae are erect the veins and the epithelium make up the roof of the lamellae when attached to hosts. The cranial vasculature of remoras is highly modified from that of other vertebrate; however, since remoras can attach to both exothermic and endothermic hosts, it is unlikely that it acts as a heat-sink. Instead, it most likely has a role in the cranial adhesive mechanism.

**Article Contribution:** This paper dwells into the soft tissue that is present in adhesive discs, which was mentioned in another study; however, they could not understand the mechanism/role it plays. The authors were able to figure out the anatomy of the cranial vasculature and how the blood vessels are interconnected to the adhesive disc and how it most likely plays a role in sticking to hosts. Although no exact function was deduced, they raised an hypothesis which could be used for studies in the future regarding how the cranial vasculature may have a role in the equalization of pressure in lamellar compartments.

Kenaley, C. P., Stote, A., Ludt, W. B., & Chakrabarty, P. (2019). Comparative functional and phylogenomic analyses of host association in the remoras (Echeneidae), a family of hitchhiking fishes. *Integrative Organismal Biology*, *1*(1). <https://doi.org/10.1093/iob/obz007>

The study objective was to resolve the phylogeny of remoras and the morphological basis of disc adhesion performance. They used a phylogenomic approach believing that hundreds of loci across several genomes can provide stronger phylogenetic signals than the few loci used in previous analyses. One prior study on this topic suggested a hypothesis that concluded the group encompassed two distinct clades. The first being a reef-generalist group that do not have any specificity for a host, and the pelagic specialists who have a strong preference for certain hosts including pelagic sharks, billfishes, and swordfish (O’Toole 2002). The authors resolved the interrelationships of the Echeneidae using a phylogenomic approach with ultra-conserved elements. They then used this to characterize the disc morphology by performing a micro-CT analysis, and also evaluated host specificity by analyzing host phylogenetic distance. They then determined which axes of disc morphological variation are associated with host diversity.

By using a novel UCE dataset with 445 loci across the genome, the authors were able to develop a phylogenetic hypothesis by recovering a monophyletic Echeneidae and monophyletic reef and pelagic group. They found that the specificity of host choice is more diverse in the pelagic group and less diverse in the reef-generalist group. These results oppose those of previous literature, which proposed that reef-generalist group would have more variability in host selection (O’Toole 2002). Furthermore, they found that the axes of disc morphospace are best explained by models that include host skin surface roughness. This means that the diversification of host is determined by the host skin surface roughness, host specialization, and hydrodynamic regime.

**Article Contribution:** I chose to include this article because it goes into why remoras choose certain hosts, which other articles although touched upon, was based more on speculation. Furthermore, this study expanded on the research of previous literature, and even found that their results were slightly different from what was believed prior. The authors suggested future research to be directed in the area of creating artificial adhesion devices that can perform well over variable rough services based on the remora disc system.

O’Toole B. (2002). Phylogeny of the species of the superfamily echeneoidea (Perciformes: Carangoidei: Echeneidae, Rachycentridae, and Coryphaenidae), with an interpretation of echeneid hitchhiking behavior. *Canadian Journal of Zoology* 80:596-623

Friedman, M., Johanson, Z., Harrington, R. C., Near, T. J., & Graham, M. R. (2013). An early fossil remora (Echeneoidea) reveals the evolutionary assembly of the adhesion disc. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1766), 20131200. <https://doi.org/10.1098/rspb.2013.1200>

The suction disc of remoras shows structural innovations within fishes. Remoras belong to the clade acanthomorphs, and they possess bizarre cranial designs that have evolved from the spinous portion of the dorsal fin of other acanthomorphs. The first remora fossil that was described was from the extinct genus +*Opisthomyzon*, which provided some insight into the origin of the group. The objective of the study is to understand the evolutionary assembly of the adhesion disc. A comparative approach was used that involved all eight species of remoras, two species of dolphinfishes, and a single species of cobia. They also analyzed osteological features of fossils and living taxa from adult specimens. The also assembled a phylogenetic dataset by analyzing the anatomical features of remoras and their close relatives, and an analysis was completed using maximum parsimony and Bayesian inference.

*+Opisthomyzon* only had six lamellar protrusions meaning there were quite a bit fewer of them in the extinct genus relative to living remoras. In addition to this, the lamellae had no pectinations other than by the median spinule, and the lamellae were found to be single rather than paired. The median spinule itself was not autogenous but instead found together with lamellae. The disc was also short relative to living remoras. The significance of these results is that it shows the evolutionary changes that occurred between when the genus was still existing to relative modern-day remoras. This can be important in determining what structures are important for adhesion within the suction disc. For example, lamellae are thought to have a function in creating a suction seal so the fact that there were fewer of them in the extinct genus relative to living remora, indicates how important this structure is in adhesion; it underwent evolutionary changes.

**Article Contribution:** This study has provided insight into evolutionary changes in the assembly of the adhesion disc found in living remoras. The adaptations have improved the ability of remoras to be able to stick on animals, and by understanding the evolutionary assembly, the importance of each structure can be deciphered. Furthermore, the authors were able to correct previous mistakes made in the classification of the extinct genus which is important in the determination of close relatives. \*Future studies can be determining the exact sequence of evolutionary changes and the time they occurred to better understand the assembly of the disc.

Gamel, K. M., Garner, A. M., & Flammang, B. E. (2019). Bioinspired remora adhesive disc offers insight into evolution. *Bioinspiration & Biomimetics*, *14*(5), 056014. <https://doi.org/10.1088/1748-3190/ab3895>

The closest relative to remoras is *Rachycentron canadum*, also referred to as black salmon or cobia. These fish lack an adhesive disc but they also display a similar behavior as they follow large fish closely and consume on extra food scraps. The authors hypothesize that the closest common ancestor of remoras and cobia employed host following which led to selective pressure that favors morphology that is reliant on low-energy costing interactions with larger marine animals. The objective of this study was to design a bioinspired adhesion disc based on fundamental principles and use it to investigate how more lamellae and spinules may lead to increased adhesive performance. The morphology of remoras was analyzed by computed microtomographic scanning. Furthermore, in designing the bioinspired remora disc, two rules were followed: the first was that attachment must be achieved passively through shear forces and secondly the lamellae needed to be removable so they could compare morphological conditions. The attachment surfaces were made using silicon molds with different roughness. Furthermore, to determine the impact of lamellar number and substrate on the adhesive force, two-way analyses of variance (ANOVA) test was used.

The ANOVA test indicated the interaction between lamella (the number of lamella) and the substrate impacted both mean maximum shear adhesive force and the mean force per spinule. Furthermore, no matter the number of lamellae, the disc always performed the best on the surfaces that had 180 and 350-grit. This is similar to the range of shark skin, meaning remoras may be able to attach the best on sharks relative to other marine animals like whales or turtles. However, there was no difference on the exerted mean shear force between smooth and rough surfaces. In regard to evolution, the results showed that more pectinated lamellae resulted in a performance advantage under shear conditions.

**Article Contribution:** The authors were able to create a bioinspired disc on their own that followed the basic principles of adhesion. This is significant in trying to understand exactly how a certain variable impacts adhesion, as they are able to manipulate their disc. For example, they could change the number of lamellae, and by doing so they found out that more lamellae did indeed result in better adhesion under shear conditions. Future research can be directed more towards how changing the number of spinules impacts adhesion.

Lee, S. H., Song, H. W., Kang, B. S., & Kwak, M. K. (2019). Remora-inspired reversible adhesive for underwater applications. *ACS Applied Materials & Interfaces*, *11*(50), 47571–47576. https://doi.org/10.1021/acsami.9b16350

Remoras cling to the host by deforming the internal shape of the adhesion disk connected to the nerve by itself. The disc has a fleshy disk lip which maintains a tight seal. When the remora attaches, the disk lip and the lamella that are connected to the nervous system become deformed which generates a pressure difference between the outside and inside of the disc. This pressure difference allows the remora to adhere to the host stably. Furthermore, the spinules have hair which increases the adhesion area and also minimizes the chance of the remora sliding off. The main objective of this study was to fabricate a polymer-based adhesive that mimics the properties of the remora suction disc and determine its performance. The mold was made using a digital light processing type 3D printer, and the master mold surface was then modulated. The structure of the adhesive was characterized using optical microscopy and scanning electron microscopy. The adhesive was then fabricated using lithography and lastly, they measured the adhesive and frictional properties of the fabrication in the water.

The RIA was able to stick onto the glass for 10 days or more, and the performance was consistent even after being used several times. The adhesion was maintained on both smooth and rough surfaces despite various different motions. The results of the study show how effective the remora adhesion disc is in remaining attached to a host, as just the remora-inspired disc was able to stay attached for more than 10 days. Furthermore, the adhesive is strong enough to withstand different motions of the host, therefore, that is not a crucial factor when it comes to remoras detaching. Instead, the remoras most likely detach mainly for food purposes. Lastly, with continued use of the disc, it still doesn’t lose its’ effectiveness.

**Article Contribution:** The authors were able to analyze the different structures of the adhesion disc and create their own fabrication which allowed them to perform various tests to measure the efficiency of the disc. Other studies mainly analyze based on phylogenetics or video evidence, so this study provides a different approach. Furthermore, they discovered the suction disc can maintain adhesion for at least 10 days, which was not researched in other studies. Future research can be directed at seeing what other surfaces the remora-inspired adhesion disc can attach to, which may provide better context on how or why they pick certain hosts.