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Bioinspired remora adhesive disc offers insight into evolution

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Abstract

Remoras are a family of fishes that can attach to other swimming organisms via an adhesive disc evolved from dorsal fin elements. However, the factors driving the evolution of remora disc morphology are poorly understood. It is not possible to link selective pressure for attachment to a specific host surface because all known hosts evolved before remoras themselves. Fortunately, the fundamental physics of suction and friction are mechanically conserved. Therefore, a morphologically relevant bioinspired model can be used to examine performance of hypothetical evolutionary intermediates. Using a bioinspired remora disc, we experimentally investigated the performance of increased lamellar number on shear adhesion. Herein, we translated fundamental biological principles into engineering design rules and show that a passive model system can autonomously achieve adhesive forces measured in live remoras in any environment. Our experimental results show that an increase in lamellar number resulted in an increase in shear adhesive performance, supporting the phylogenetic trend observed in extant remoras. The greatest pull-off forces measured for our model were on surface roughness on the order of shark skin and exceeded those measured for live remoras attached to shark skin by almost 60%. Overall, relative to fossil remoras and their closest ancestor, extant remoras exhibit a morphology indicative of selection for enhanced shear adhesive performance.

1. Introduction

Remoras (family Echeneidae), are fishes that attach to sharks, whales, billfishes, turtles, ships, and occasionally scuba divers [1–6], thereby adhering under a wide range of fluid drag conditions in addition to a variety of surfaces. The remora is the only marine organism to maintain attachment to fast-moving hosts of varying roughness and compliance while retaining the ability to easily release, a technological feat not yet achieved by man-made devices. Other 'sticky' organisms, including adhesive fishes, attach to stationary objects [7–11] or require permanent adhesive mechanisms, such as glues, for attachment to moving objects [12, 13].

Remora attachment is accomplished by their cranial adhesive disc which evolved from dorsal fin spines (figure 1) [14–16]. The adhesive disc consists of a series of pectinated bony lamellae that rotate from a flat to erect position; doing so engages hundreds of small spinules that project from the lamellae with the host surface to generate friction [15, 17]. In addition, the lamellae are surrounded by a soft tissue lip which creates a suction seal when the lamellae rotate [18, 19]. Importantly, the lamellae are oriented in such a way that shear forces applied to the disc passively enhance anterior rotation of the lamellae, thereby increasing the spinule contact and local friction coefficient of the disc [15, 17, 20].

The evolution of such a novel feature is something of a mystery especially in terms of its complexity as a hierarchical mechanism. In terms of evolutionary fitness, there are numerous advantages afforded to remoras by being able to attach to larger host organisms. These include reduced predation, reduced locomotor costs, increased chance of meeting conspecifics for mating, increased food availability (e.g. host parasites or food droppings), and facilitated ventilation [6]. The closest relative of remoras, the cobia or black salmon (*Rachycentron canadum*), lacks an adhesive disc but exhibits close-following behavior to larger fishes and feeds off food droppings [15]. Thus, cobia may also

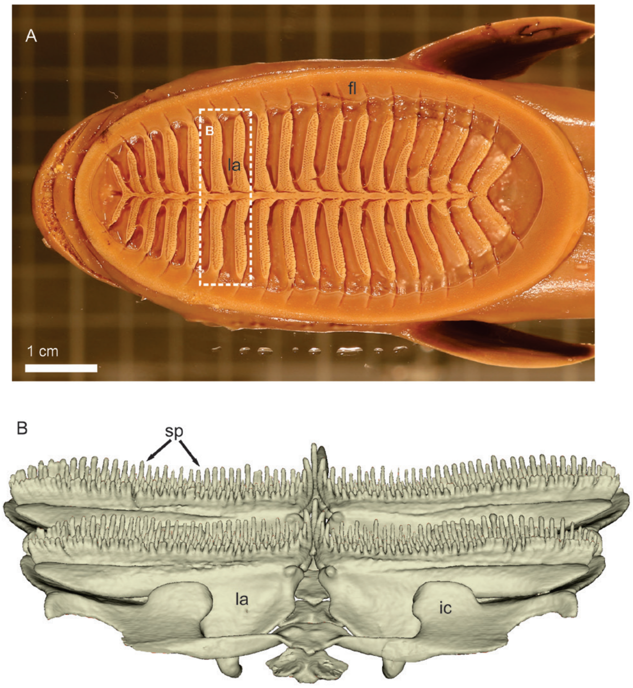

Figure 1. Functional morphology of the adhesive disc of *Remora remora*. (A) Dorsal view of remora disc when attached to clear plexiglass, dashed box shows orientation of *B*; *fl*, fleshy lip; *la*, pectinated lamella. (B) 3D reconstruction of μCT scan of *Remora remora* disc, head-on view; *ic*, intercalary plate; *sp*, spinules.

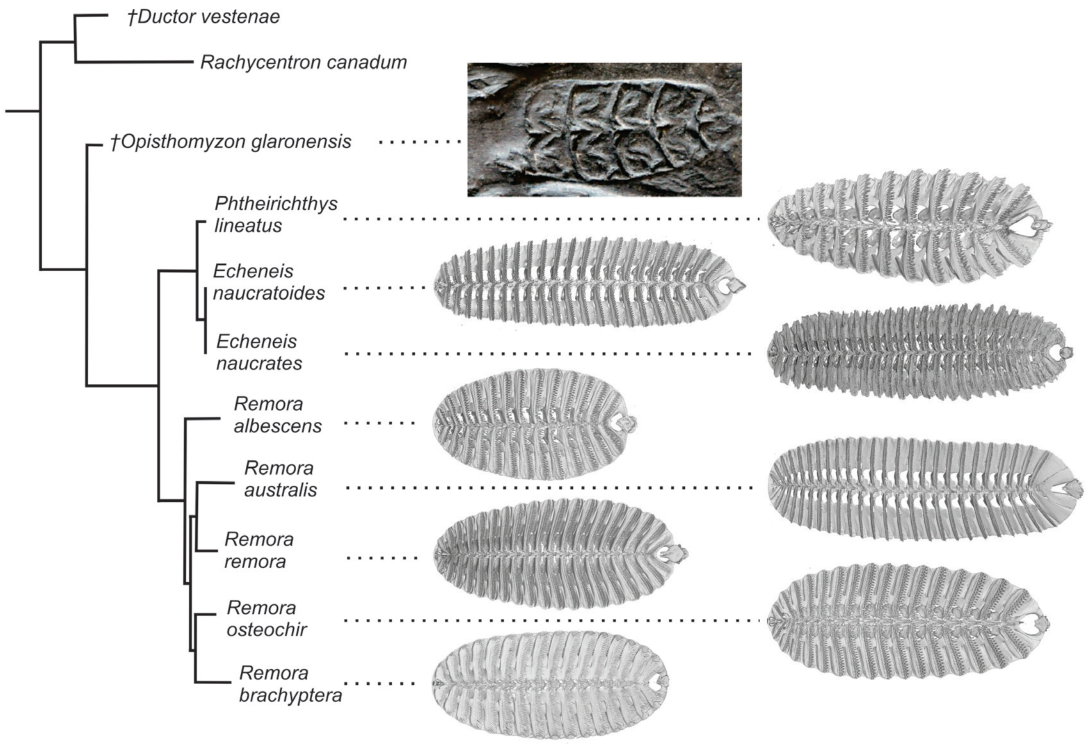

Figure 2. Relationship of remoras and their relatives. Phylogeny and image of *Opisthomyzon glaronensis* from [14], modified with permission. Dorsal view of remora discs from μCT scans.

benefit from a selective advantage in fitness if they are able to stay close enough to the host to reduce drag, avoid predation, and increase conspecific interactions. We hypothesize that the closest common ancestor of remoras and cobia also employed host following and this resulted in selective pressures favoring morphology that increased secure, low-energetic cost interaction with large swimming hosts.

The functional mechanisms underlying the origin of attachment in early remoras is not known. An early fossil remora from the Oligocene (approximately 32-25 mya), †*Opisthomyzon*, was identified as a stemgroup echeneid possessing morphological qualities of both extant remoras and outgroup taxa (figure 2). Notably, †*Opisthomyzon* possessed six lamellae, however these lacked spinules and the disc as a whole was located more posteriorly than in modern remoras [14, 21]. How, or to what, remoras may have first attached is difficult to deduce: sharks (400 mya), sea turtles (245 mya), and cetaceans (50-35 mya) all evolved before remoras themselves [22–24]. There are eight extant species of remoras and morphological variation among these is minimal. There is a clear increase number of lamellae and overall morphological complexity through time (figure 1). We hypothesize that this increase in lamellar number is the result of selection for increased adhesive performance. An increase in number of lamellae would support an increase in number of spinules to enhance shear adhesion as well.

While it is not possible to directly test the functional mechanisms driving adhesion in fossil remoras, the physical principles of friction, suction, and shear are constant irrespective of time. Bioinspired model organisms constructed to replicate the biomechanical performance of living organisms offer an opportunity to experimentally study extinct organisms [25]. The goal of this research was to design an autonomous bioinspired remora disc based on fundamental principles and to use the disc to experimentally investigate the effect of increasing the number of lamellae, and therefore spinules, to determine if there was a selective advantage in shear adhesive performance.

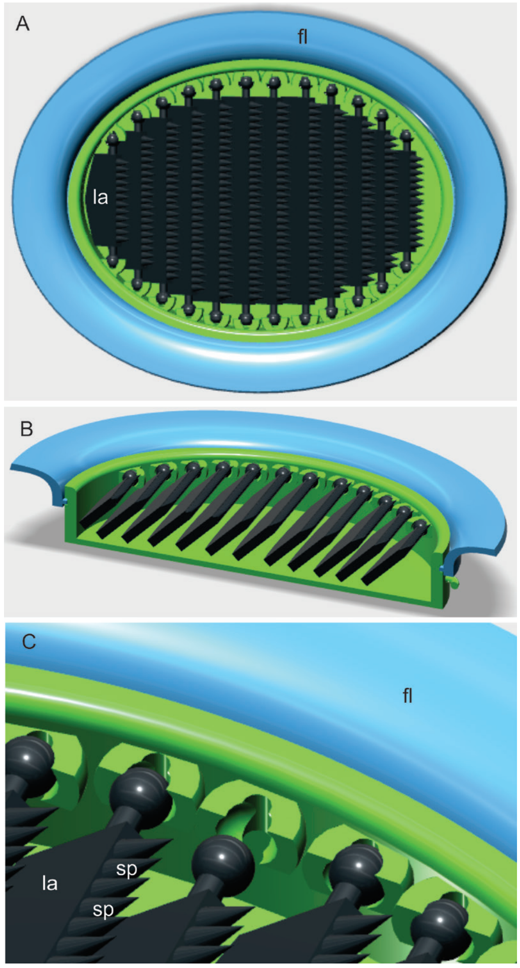

Figure 3. Bioinspired remora disc design. (A) Dorsal view of bioinspired disc. (B) Cutaway view of disc showing lamellae. (C) Close-up view of lamellar attachment joints. *fl*, fleshy lip, blue; *la*, pectinated lamellae, black; *sp*, spinule, black; disc case, green.

2. Methods and materials

2.1. Remora disc morphology

Computed microtomographic (μCT) scanning of the eight known species of extant remoras using a Bruker Skyscan 1275 (Microphotonics, Inc.) at the New Jersey Institute of Technology Otto York Bioimaging facility produced data for 3D examination of the remora disc morphology. All scans were conducted at 75 kV and 130 μA with voxel sizes ranging from 12–26 μm. Species studied included *Phtheirichthys lineatus* (MCZ 33448, 18.5 cm total length, TL), *Echeneis naucratoides* (MCZ 8678, 24.7 cm TL), *E. naucrates* (MCZ 8663, head only, 7.9 cm), *Remora albescens* (MCZ 31364, 6.7 cm TL), *R. australis* (MCZ 8685, 10.8 cm TL), *R. remora* (MCZ 83212, head only, 9.3 cm), *R. osteochir* (MCZ 43246, head only, 10.4 cm), and *R. brachyptera* (MCZ 8668, 17.7 cm).

2.2. Model design and fabrication

Design of the bioinspired remora adhesive disc followed two rules: (1) to be biologically relevant, attachment had to be achieved and maintained passively through shear forces [15, 17], and (2) to allow for comparison among multiple morphological conditions, lamellae needed to be removable with as few variables as possible. Our reduced-variable, multi-configuration comparative model (figure 3) was created in 123D design (version 14.2.2, Autodesk, Inc.). A ball-in-socket joint on both ends of the lamellae permitted uniaxial motion and easy removal. Fabricating the lamellae to sit parallel to one another in series allowed ease of changing the array and number of the lamella in the model. The lamellae were created with a wide U-shape ventrally to inhibit over-rotation and allow for full engagement of the lamellae with the substrate.

The model design was optimized for 3D printing using PreForm (version 2.17.1, Formlabs, Inc.) and printed as two separate components in the Form 2. The lip was printed at 50 μm layer height in flexible material (V2, FLFLGR02; FormLabs, Inc.; maximum tensile strength, 7.7–8.5 MPa, fracture strain 75%–85%, shear strength 13.3–14.1 kN m^{-1}) to allow for viscoelastic deformation while generating a seal to the substrate. The disc and lamellae were printed at 25 μm layer height in color (V1, FLGPCB01; FormLabs, Inc.) and grey resin (V4, FLGPGR04; FormLabs, Inc.), respectively; both had the same material properties (maximum tensile strength 65 MPa, fracture strain 6%, Young's modulus 2.2 GPa). The lip was sealed into a groove on the disc base using silicone. The mass of

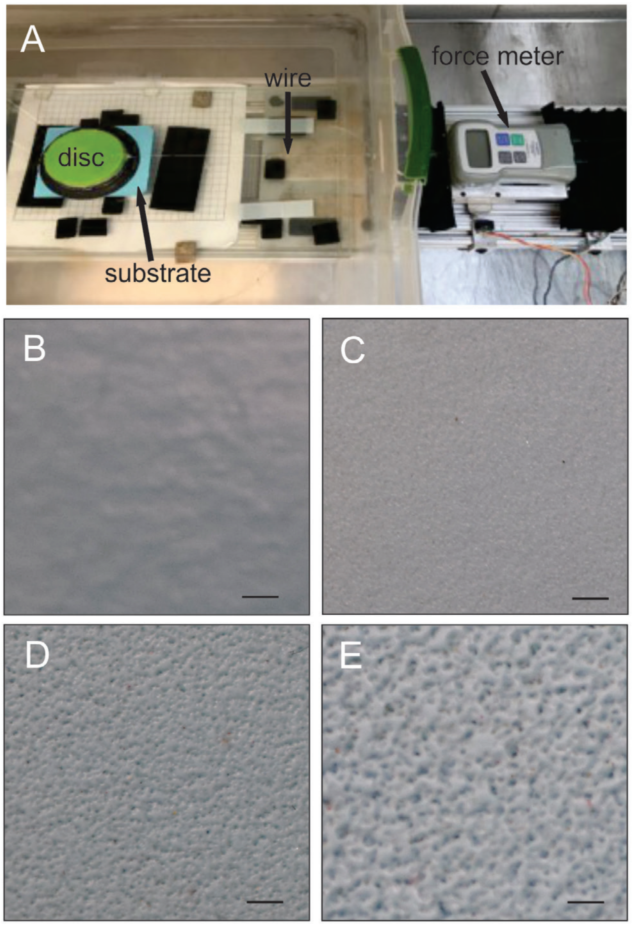

Figure 4. Testing apparatus and host surfaces. (A) Testing apparatus. Testing surfaces: (B) smooth (level air-cured), (C) 350 grit, (D) 180 grit, (E) 100 grit. Scale bars are 1 mm.

Table 1. Analysis of variance table for mean maximum shear adhesive force as a function of lamellar number, substrate, and the interaction between lamellar number and substrate.

Source	DF	Sum of squares	Mean square	*F* ratio	*P*
Lamellar number	4	547.4442	136.8611	20.0518	<0.0001[a]
Substrate	3	454.3330	151.4443	22.1884	<0.0001[a]
Lamellar number ∗ substrate	12	294.1107	24.5092	3.5909	0.0011[a]
Error	40	273.0152	6.8254	—	—

[a] Indicates a significant *P* value ($P < 0.05$).

Table 2. Analysis of variance table for mean force per spinule as a function of lamellar number, substrate, and the interaction between lamellar number and substrate.

Source	DF	Sum of squares	Mean square	*F* ratio	*P*
Lamellar number	3	0.2808	0.0936	283.2804	<0.0001[a]
Substrate	3	0.0413	0.0138	41.6186	<0.0001[a]
Lamellar number ∗ substrate	9	0.0417	0.0046	14.0341	<0.0001[a]
Error	32	0.0106	0.0003	—	—

[a] Indicates a significant *P* value ($P < 0.05$).

the complete disc ranged from 32.4 g (0 lamellae) to 45.6 g (12 lamellae).

2.3. Substrates

Silicon molds of different roughness were cast to use as comparable attachment surfaces. We chose to use a commercially available urethane elastomer (Dragon Skin, Smooth-On Inc. Easton, PA, USA) rather than natural tissues to guarantee homogeneity and reduce dependence on hydration levels, both of which are frequently cited as difficulties in working with biological tissues [26]. Each mold was cast from

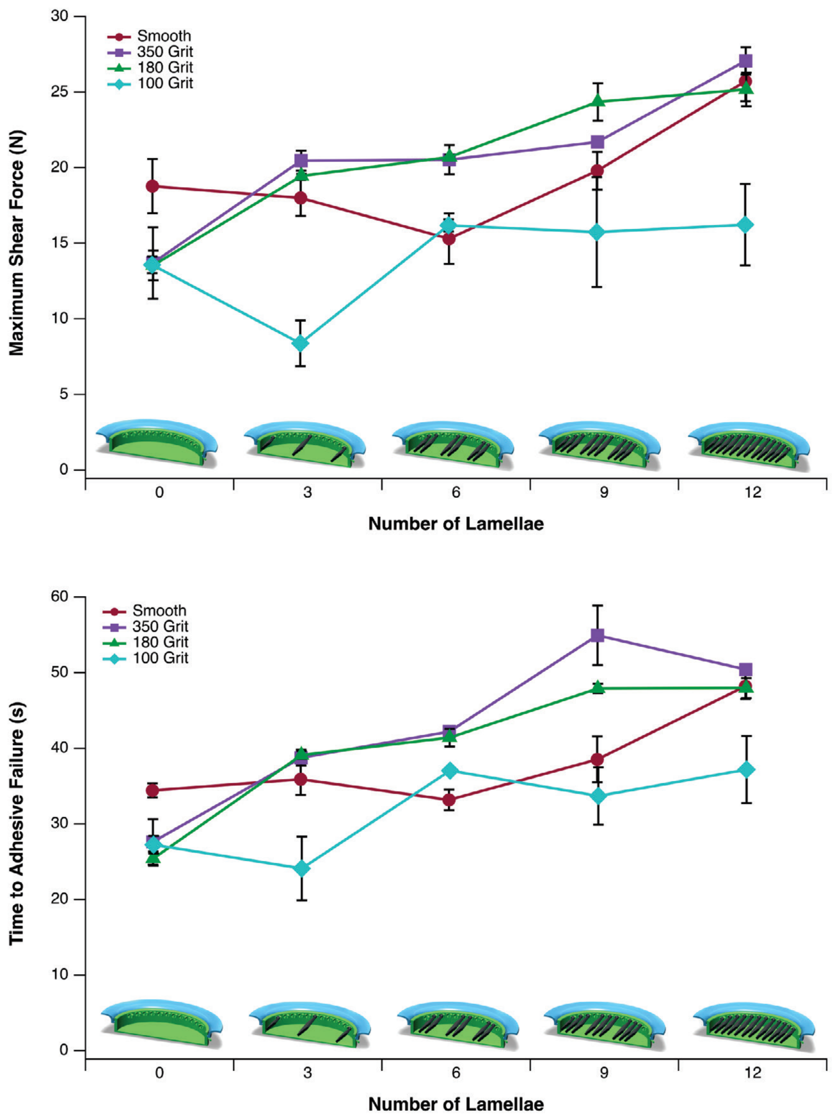

Figure 5. Shear force and time to failure of lamellar configurations on different roughness surfaces. Error bars are ±SE.

different sanding paper surfaces and were sequentially named smooth (level cured surface), 350-grit, 180-grit and 100-grit. As a biological comparison, sharkskin roughness varies by species but is in the approximate range of 240-grit [17].

2.4. Data collection

Pull-off force experiments were conducted as in [27]. The disc and the silicon molds with varying surface roughness were attached to a glass substrate firmly anchored by Velcro® (Velcro USA Inc., Manchester, NH USA) in the bottom of a plastic tub of water by applying a strong normal force to expel air from under the disc. Water completely covered the flexible lip of the disc. The disc was attached to a motor driven force gauge (Shimpo FGV-10×) capable of sensing up to 50 N via a string that passed through a small circular hole in the tub (figure 4(A)). The motorized force sensor applied a shear load at a constant 0.08 cm s^{-1}. Data acquisition was initiated in under 5 s from time of disc attachment in all trials and force data was recorded at a sample rate of 20 samples s^{-1}. A trial concluded when slippage occurred, observed visually and evident by a rapid decrease in shear force. Digital output was recorded in a LabVIEW® program. Each of the five lamellar conformations was tested three times on each of the four substrates. Maximum shear force or pull-off force was the highest value recorded between the start of a pull and the point at which slippage occurred. Mean shear force was the average of maximum shear or pull-off forces measured for a given figuration on a given substrate.

2.5. Statistical analyses

The impact of lamellar number and substrate on mean maximum shear adhesive force and mean force per spinule were evaluated using two-way analyses of variance (ANOVA). The dependent variables were either mean maximum shear adhesive force or mean force per spinule and the independent variables were lamellar number, substrate, and the interaction between lamellar number and substrate (lamellar number ∗ substrate). In the case of a significant whole model, a Tukey's Honest Significant Difference test was performed post hoc to determine significant differences between groups. Data conformed to the assumptions of ANOVA. All statistical analyses were performed in JMP Pro 14 (SAS Institute Inc., Cary, NC USA).

3. Results

From the ANOVA results we found that lamellar number, substrate, and their interaction significantly impacted both mean maximum shear adhesive force and mean force per spinule (tables 1 and 2). With any number of pectinated lamellae in place, the disc performed best on surfaces of 180 and 350-grit, approximating the range of shark skin ($P < 0.0001$). However, mean shear force on these surfaces was not significantly different compared to that of the smooth surface (smooth versus 180-grit: $P = 0.6396$; smooth versus 350-grit: $P = 0.6119$) (figure 5). For all rough surfaces, the 12-lamellae condition maintained attachment under the greatest shear forces applied ($P < 0.05$ when compared across all of the surfaces). In the 12-lamellae condition mean maximum pull-off force was achieved at 27.1 ± 0.9 against the 350-grit substrate (table 3). The 9-lamellae configuration achieved the longest hold duration of all trials (54.9 ± 4.0 s) while a force of approximately 21.7 ± 0.3 N was applied during attachment to the 350-grit surface. The significant interaction between lamellar number and substrate suggests that the disc responds to surface roughness in different manners depending on the number of lamellae present.

Lamellar number treatments showed a roughly linear association of increasing lamellar number to both pull-off force and attachment duration on the 350 and 180-grit substrates (table 3 and figure 5). However, the relationship between lamellar number and adhesive force was not linear on the smooth and 100-grit substrates. On the smooth surface, the 6-lamellae condition performed at a lower maximum force compared to the 12-lamellae condition ($P = 0.0024$), but at a similar pull-off force to the 0-lamellae configuration on other surfaces (all comparisons $P > 0.05$), potentially indicating a correlation between spinule height and roughness. The disc had a relatively lower adhesive force on the 100-grit surface under all lamellar configurations ($P < 0.0001$ in all cases), presumably because a good suction seal was not achieved on this surface. Therefore, the 100-grit surface represents the condition of adhesion with lamellae only without a fleshy lip producing a seal; under this condition (i.e. on the 100-grit surface) there was no significant variation in adhesive force as a function of lamellar number ($P > 0.05$ in all comparisons).

Attachment force relative to the number of spinules in a given trial was calculated to elicit the frictional contribution to disc adhesion (figure 6). On the smooth, 350-grit, and 180-grit substrates, the 3-lamellae condition exhibited the highest force per spinule ($P < 0.0001$ in all comparisons); approximately 0.3–0.35 N was concentrated on each of the 61 spinules. The lower force per spinule for the 61 spinules on the 100-grit substrate is correlated to half the force being generated as relative to the other substrates overall. However, for all rough surfaces, in the 6-lamellae condition, 0.1–0.15 N force was distributed among the 146 spinules and an increase in the number of spinules (here, 220 and 294) did not show an appreciable decrease in force per spinule (0.05–0.1 N). This suggests that after a certain number of spinules, in this case 146, secure attachment by ratcheting friction is achieved and any additional spinules cumulatively increase the overall frictional force generation in the disc.

Incremental addition of lamellae decreased disc volume by approximately 1.04 ± 0.07 ml, which was calculated to be equal to a static pressure loss of approximately 0.28 kPa per lamella. Total pressure (P_t), the additive effect of static and dynamic pressure under shear, was calculated for the disc under each of the lamellar conditions. Based on this, the maximum possible suction pressure for each lamellar configuration was as follows: 0-lamellae, −51.24 kPa; 3-lamellae, −51.31 kPa; 6-lamellae, −50.49 kPa; 9-lamellae, −49.91 kPa; and 12-lamellae, −46.88 kPa. An increase in lamellar number necessarily requires a tradeoff in lamellar compartment volume, e.g. the volume between lamellae, and an overall reduction in the fluid volume of the disc in a

Table 3. Results from pull-off experiments. Maximum force (strength) at pull-off and average time attached until failure are reported as averages with standard error.

Treatment	Substrate roughness	Maximum force (N)	Time to failure (s)
0-lamellae	smooth	18.8 ± 3.1	34.4 ± 1.6
	350-grit	13.7 ± 4.1	27.6 ± 5.2
	180-grit	13.5 ± 1.7	25.4 ± 1.6
	100-grit	13.6 ± 1.0	27.2 ± 2.0
3-lamellae	smooth	18.0 ± 2.1	35.9 ± 3.6
	350-grit	20.5 ± 1.1	38.8 ± 1.8
	180-grit	19.5 ± 0.2	39.1 ± 0.9
	100-grit	8.4 ± 2.6	24.1 ± 7.3
6-lamellae	smooth	15.3 ± 2.9	33.2 ± 2.4
	350-grit	20.5 ± 1.7	42.2 ± 0.9
	180-grit	20.7 ± 0.3	41.4 ± 2.0
	100-grit	16.2 ± 0.7	37.1 ± 0.6
9-lamellae	smooth	19.8 ± 2.2	38.5 ± 5.3
	350-grit	21.7 ± 0.5	54.9 ± 6.9
	180-grit	24.4 ± 2.2	47.9 ± 1.0
	100-grit	15.7 ± 6.3	33.7 ± 6.6
12-lamellae	smooth	25.7 ± 2.3	48.2 ± 2.9
	350-grit	27.1 ± 1.6	50.4 ± 0.6
	180-grit	25.2 ± 1.9	48.0 ± 2.2
	100-grit	16.2 ± 4.6	37.2 ± 7.7

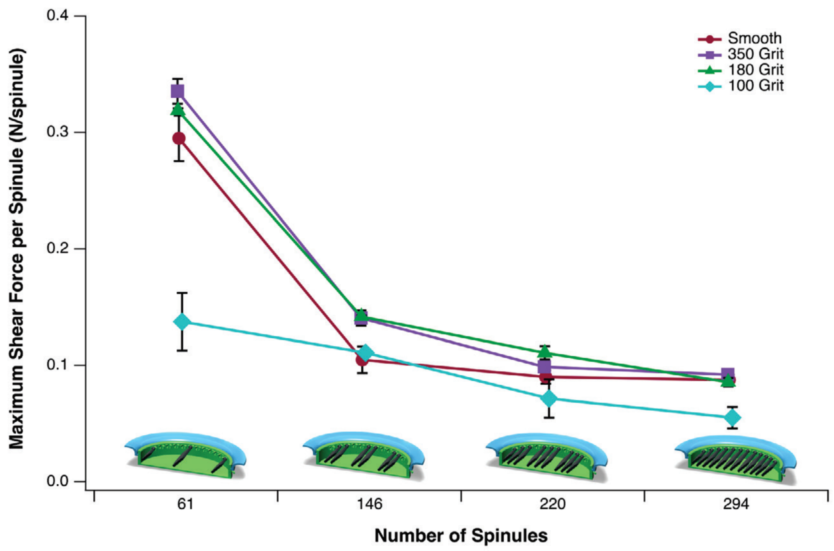

Figure 6. Maximum shear force per spinule as a factor of number of spinules and surface roughness. Error bars are ±SE.

constrained disc shape. As a result, the maximum suction force that can be generated, derived from the greatest pressure differential that can be achieved during adhesion, is reduced when increasing lamellae. The maximum possible suction forces generated by our model under all lamellar conditions were comparable to that reported in remoras attached to shark skin (−46.6 kPa, 15).

4. Discussion

Previous work estimating pull-off forces for live remoras found that 17.4 N and 11.2 N of force were required to dislodge the disc from sharkskin and smooth plexiglass, respectively [15, 17]. Our disc maintained attachment up to a maximum shear force of approximately 27 N for surfaces encompassing the range of shark skin [17], and 25.7 N on the smooth surface. Overall, our disc model showed an increase in attachment performance was correlated with an increase in lamellar, and thus spinule number. Interestingly, on extremely smooth and rough surfaces, a transition between suction and friction dominated adhesion was observed (figures 5 and 6). On the smooth surface, too few lamellae performed the same as no lamellae at all, suggesting that little frictional benefit was achieved and adhesion was mostly due to suction; however, shear adhesive force increased relatively linearly for the 9 and 12-lamellae conditions indicating a threshold of spinule contact had been met and a positive correlation between spinule number and pull-off force existed. On the roughest surface, too few lamellae performed poorly under suction-dominate conditions, as the silicone disc lip likely lacked the viscoelastic properties of tissue found in the remora disc lip and did not conform to the surface asperities well enough to decrease permeability, despite an adequate pressure decrease of greater than 30 kPa to generate suction [18]. Despite an increase in spinules, the pull-off performance on the roughest surface plateaued at a peak of about 16 N. This was most likely because with sufficiently long wavelength asperities, there is a reduction in spinule-slope interaction, making too rough a surface effectively equivalent to flat surface in terms of local friction [17].

With regards to the evolution of the remora adhesive disc, we have shown here that the increase of pectinated lamellae results in a performance advantage under shear conditions. Examination of extant remora (figure 2), illustrates that the increase in lamellar number resulted in a change in disc shape as well, thereby increasing the disc volume with each additional lamella. This negates the tradeoff inherent in our reduced-variable, multi-configuration comparative model with the additive benefit of increased maximum possible suction pressure concurrent with increasing friction via lamellar and spinule number. Although current fossil specimens, like †*Opisthomyzon*, do not provide substantial evidence for the evolution of a soft tissue lip coincident with the appearance of lamellae, we can at least surmise that friction-based engagement with another body underwent performance-driven selection in shaping the remora disc [14, 21]. In addition, it is hypothesized that spinules evolved after lamellae [14], thus supporting selection for shear adhesive force. Under these conditions, it is likely that the first remora hosts may not have had smooth skin, as suction necessitates a viscoelastic seal on the disc perimeter. Instead, remoras likely first adhered to an organism with a surface roughness similar to sharks.

Our remora disc design demonstrated a fundamental aspect of the adhesive mechanism of live remoras: once engaged, attachment is essentially a passive mechanism. This is particularly true under shear conditions that are naturally occurring as a result of host locomotion. Importantly, for bioinspired design this means that underwater attachment is possible without an extensive amount of engineering for active control (e.g. multiple actuators and pneumatic suction, [28]). Thus, our disc is ideal for applications where low-cost, rapid-production devices are desirable, such as in geo-sensing tags for the ecological study of marine organisms. By relying on the physics of remora adhesion and reducing the need for active control mechanisms, we have also kept the adhesive disc extremely light and low-profile. This design reduces the parasitic drag on a potential host organism as well as eliminating attachment loss due to electrical failure of submerged actuating components. Finally, we demonstrated that there is an optimal range of number of lamellae for maximizing attachment force, which is useful for efficient production of discs for custom use.

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Author contributions

BEF conceived of the project; KMG designed the model; KMG, AMG, and BEF designed experiments; KMG and AMG conducted experiments; KMG, AMG, and BEF analyzed the data and wrote the manuscript.

Competing interests

The authors declare no competing interests.

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