Appendix 1

Stators

While all stators use ion gradients to drive their rotation, the specific ions used can differ between stators. Most flagellated bacterial species use just one type of stator, commonly either H^+-driven MotAB, Na^+-driven PomAB, or Na^+-driven MotPS. For example, H^+-driven MotAB is used by *E. coli* and *S. enterica*, while Na^+-driven PomAB is used by *Vibrio* species.[1]

At least 65 bacterial species use more than one type of stator.[2] For example, *Shewanella oneidensis* MR-1 has a single polar flagellum driven by both MotAB and PomAB.[3] Likewise, *Bacillus subtilis* uses a mix of MotAB and MotPS to drive each of its flagella.[4] *S. oneidensis* and *B. subtilis* can regulate what proportion of each type of stator is engaged in their motor(s) to adjust the proportion of each ion used (see part 3).[5,6]

Pseudomonas aeruginosa also has two stators, MotAB and MotCD, both H^+-driven, which drive a single polar flagellum.[7] MotAB can produce higher torque in aqueous environments while MotCD is used for swimming in highly viscous environments.[8,9] Conversely, *Aeromonas hydrophila* has two stator types (PomA1B1 and PomA2B2, both Na^+-driven) that drive a single polar flagellum.[10,11] PomA1B1 may be preferably used in low Na^+ concentrations.[10]

There are also species with three, or even four, distinct types of stators, though these have not been characterized in detail.[2] There are many species with more than one stator type, stator systems of which have not been studied, leading to greater potential for more to be discovered in this area.[10]

Having two types of stators with different properties driving a single motor allows for more control over the motor's output (see part 3 for how stators are regulated to control motor output). Different stator types can also integrate into different motors. In *Vibrio* species with polar and lateral flagella, the polar flagellum/flagella use PomAB stators and the lateral flagella use MotAB stators.[12,13]

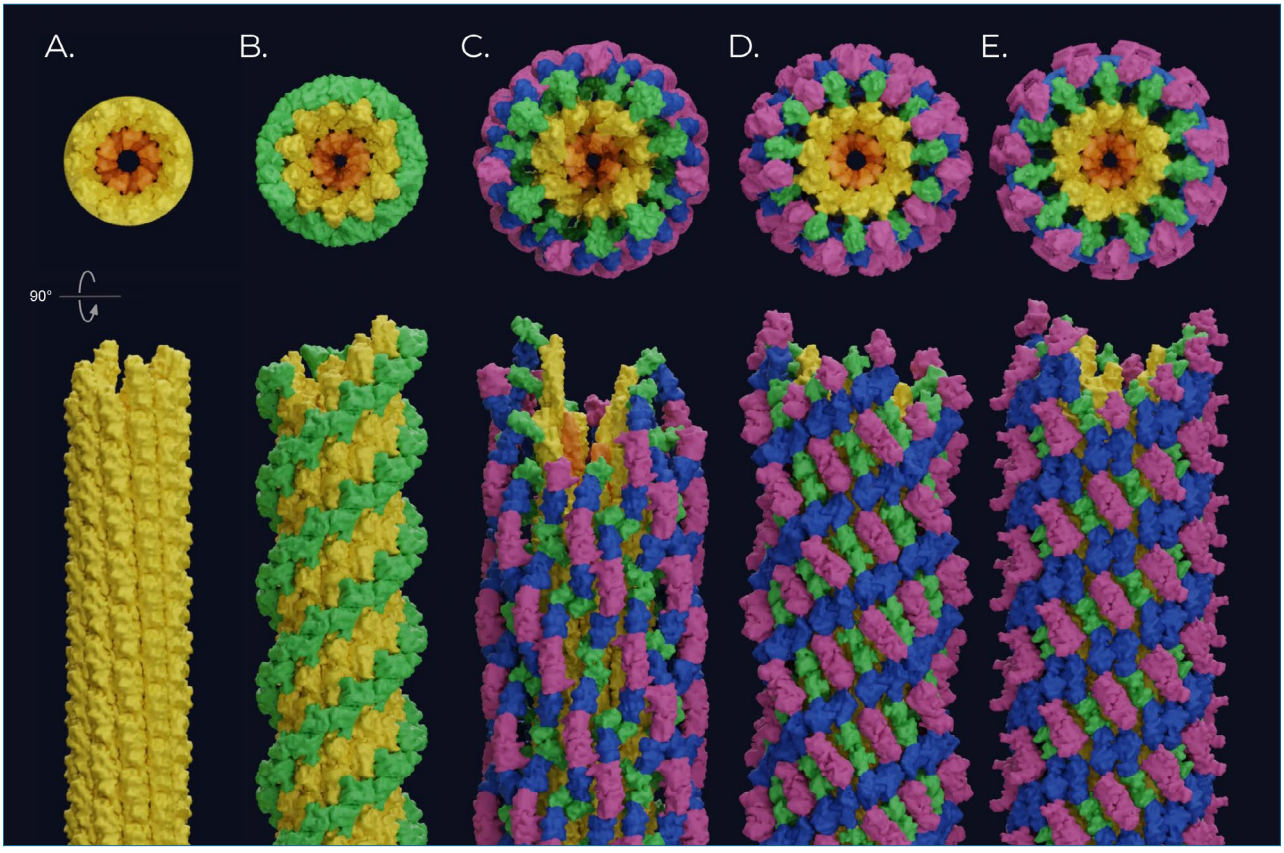


Figure 7. Molecular surface representations of diverse flagellar filament structures coloured by domains (orange = domain 1; yellow = domain 2; green = domain 3; blue = domain 4; pink = domain 5). (A) *C. crescentus* filament (PDB ID: 6XKY) with no outer domains, (B) *Sinorhizobium meliloti* filament with outer domains in a screw formation (PDB ID: 7SN9), (C) *E. coli* O127:H6 filament with outer domains forming tetramers to form a sheath (PDB ID: 7SN7), (D) *Achromobacter sp.* filament with outer domains forming tetramers to form a sheath (PDB ID:7SQD), (E) *E. coli* O157:H7 filament with outer domains forming dimers to form a sheath (PDB ID:7SN4)

Stators can also be driven by more than one ion gradient. For example, the MotPS stators of *Bacillus alcalophilus* has been reported using ion gradients of Na^+, K^+, or Rb^+.[14] A *Paenibacillis* species isolated from a hot spring with high Ca^{2+} concentration was reported to use Ca^{2+}, Mg^{2+} and Sr^{2+} gradients to drive motility.[15]

As mentioned in the next paragraph, the number of stators engaged in flagellar motors differs between species.

Central gear

The diameter of the central gear in *Caulobacter crescentus* is 34 nm, in *E. coli* and *S. enterica* is ~40 nm, in *C. jejuni* and *Helicobacter hepaticus* is 49 nm, and in *Treponema primitia* is 57 nm.[16] Polar and periplasmic flagella often have a larger central gear than peritrichous flagella.[17] This larger central gear allows more stators to be engaged and positions the stators further away from the central axis of the motor, allowing for greater torque to be produced (compare figure 1b with 1c).[18,19]

In Part 1, it was stated that the central gear is made of FliG, FliM, and FliN. In some species, like *Acetonema longum, B. subtilis, Helicobacter pylori, T. primitia, H. hepaticus, C. jejuni and S. enterica*, a large protein called 'FliY' is used in place of, or alongside, FliN.[16,20,21] FliY shares similarities with both FliM and FliN.[22] Interestingly, binding of the chemotaxis protein CheY to the central gear in *B. subtilis* causes the central gear to switch from a clockwise to a counter-clockwise rotation. The opposite occurs in Gram-negative species (e.g., *E. coli*) (see part 4).[21] FliY is likely to mediate this switch since the *B. subtilis* FliY N-terminal has a CheY-binding motif.[23] The *B. subtilis* FliY middle domain functions as a phosphatase that dephosphorylates the chemotaxis protein CheY to remove it from the central gear.[24]

B. burgdorferi has two FliG homologues, FliG1 and FliG2.[25] The central gears of the motors at one end of the cell contain both FliG1 and FliG2, while the central gears of the motors at the other end of the cell contain only FliG2.[26] This asymmetry may explain how the motors at either end of the cell can rotate in opposite directions when they are under the control of the same navigation system. It is currently

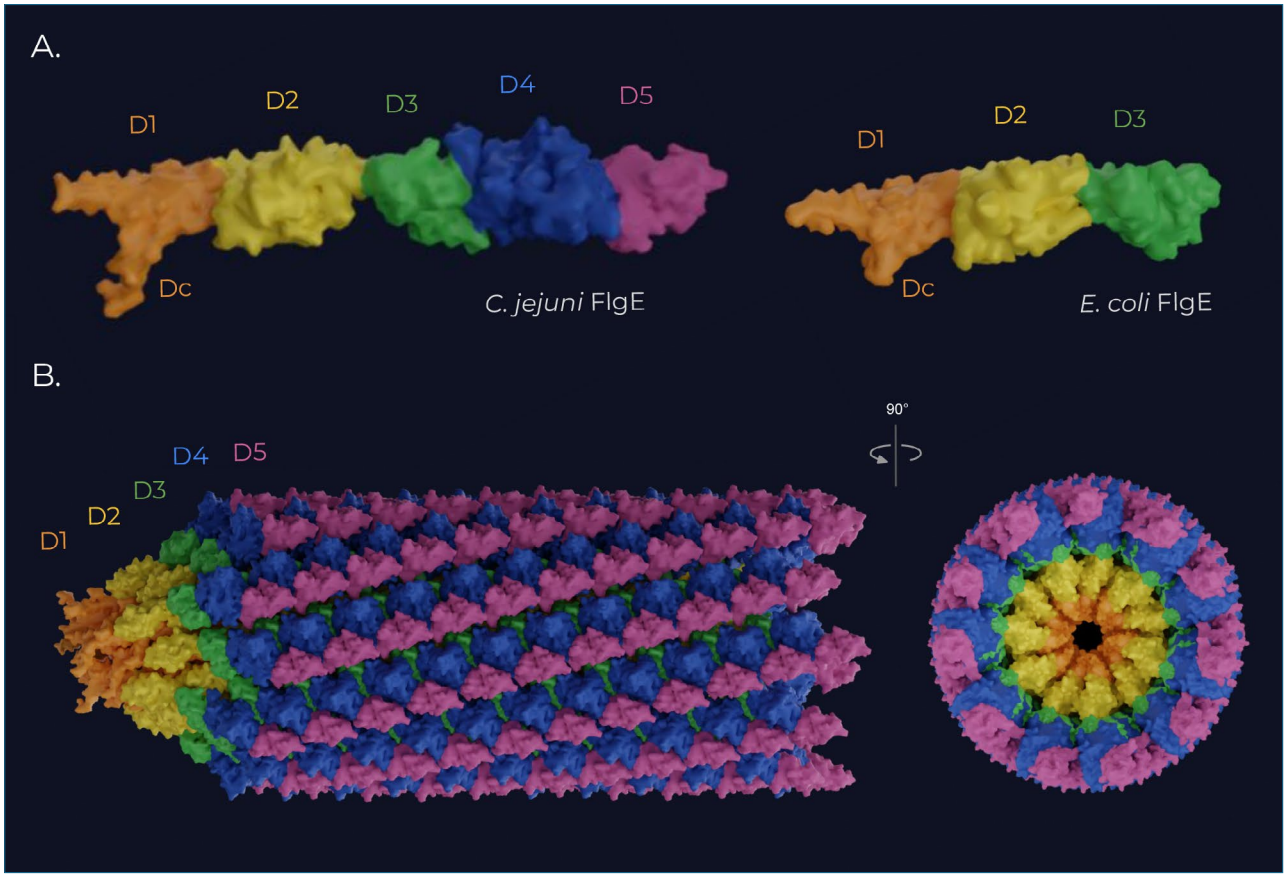


Figure 8. *C. jejuni* universal joint/Hook (PDB ID: 5JXL[38]) coloured by domains (orange = domain 1; yellow = domain 2; green = domain 3; blue = domain 4; pink = domain 5). (A) Single monomer of universal joint protein, FlgE, from *C. jejuni* (left) and *E. coli* (right): note, the length of the Dc portion of the D1 domain in *C. jejuni* is longer than in *E. coli,* giving the *C. jejuni* hook more rigidity. (B) *C. jejuni* universal joint structure.

unknown how FliG1 localizes to only one end of the cell during motor construction.

FliM and FliN in the polar motors of *V. parahaemolyticus* have unique charged domains that are absent from the lateral motors of *V. parahaemolyticus*.[27] The reason for this difference is not yet known, but the uniquely charged C-terminus of FliM is essential for motility.[27]

Universal joint

The universal joint (sometimes called the 'hook') transmits the rotation of the flagellar motor to the propeller filament, and in polar flagella facilitates turning manoeuvres (see part 3). The universal joint of *C. jejuni* is more rigid than in *E. coli* likely due to an extension of a universal joint protein (FlgE) domain called 'Dc' (figure 8).[28] The FlgE of *C. jejuni* and related bacteria also have unique extra domains not found in other species (figure 8). These extra domains give the universal joint of these species more stability and robustness, making it less likely to break.[29] It is worth noting that the universal joint-filament junction protein (FlgK) in *C. jejuni* has a different structure compared to that of FlgK in *S. enterica*, likely due to the design constraints imposed by the much larger FlgE.[30]

FlgE subunits are bound to one another through non-covalent bonds. Spirochaete FlgE subunits are also connected via a covalent crosslink, which makes the universal joints of Spirochaetes much stronger than those of other species.[31]

Propeller filament

Rotating screw-shaped flagellar filaments function as propellers. The flagellin proteins making up flagellar filaments have inner and outer domains (figure 9). The inner domains (forming the inner core of the filament, shown in orange and yellow in figure 7) are made from the terminal regions of flagellins and are very similar among species. In contrast, the outer domains are very diverse, leading them to be termed the 'flagellin hypervariable region' (figures 7 and 8).[32] A 2017 study identified 61 flagellin outer-domain families.[32] A 2020 study analyzed all available full-gene bacterial flagellin sequences with MMseqs2 and found that

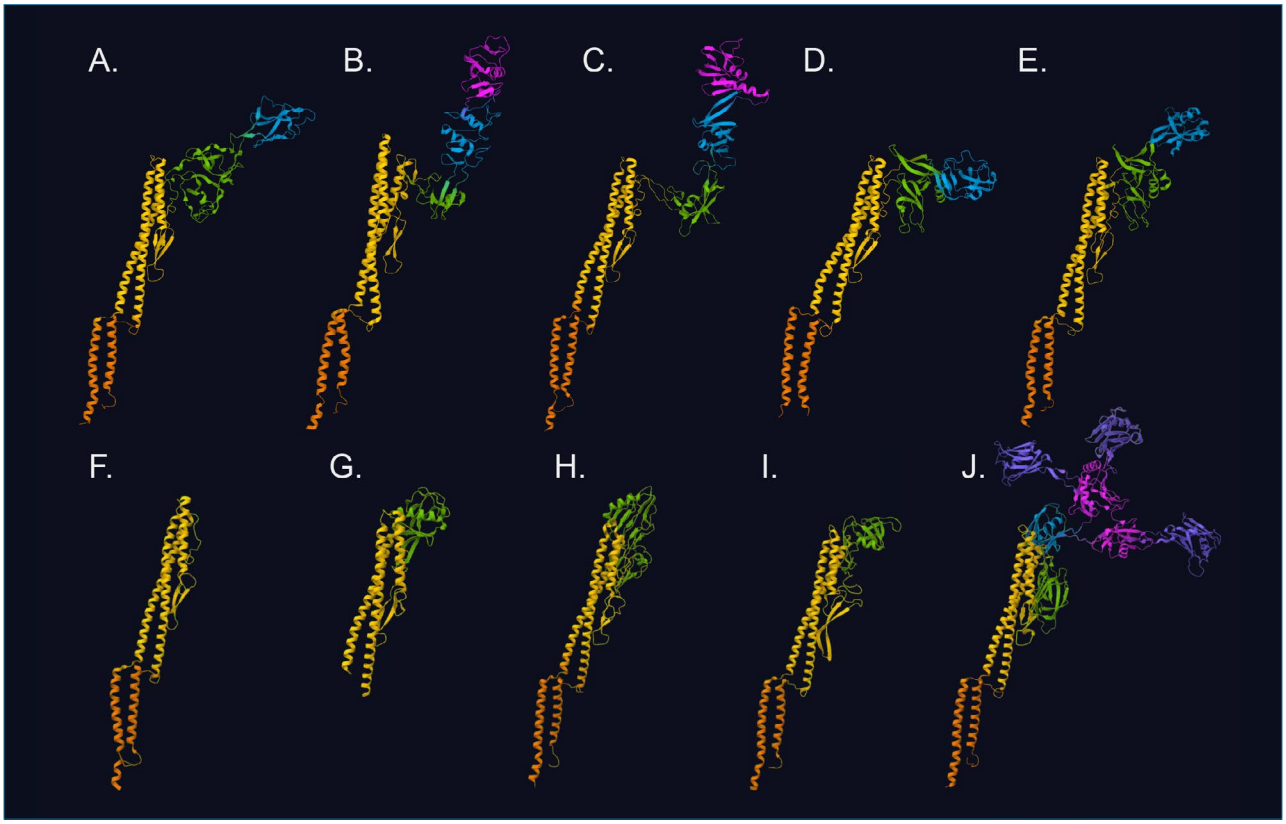


Figure 9. Diversity in flagellin structure and size coloured by domains as in figure 6 (protein graphics made in Mol*[62]). (A) FliC from *E. coli* K-12 (AlphaFold prediction: P04949), (B) FliC from *E. coli* O127:H6 (PDB ID: 7SN7[31]), (C) FliC from *E. coli* O157:H7 (PDB ID: 7SN4[31]), (D) FliC from *Salmonella* (PDB ID: 3A5X[64]), (E) FljB from *Salmonella* (PDB ID: 6JY0[65] and AlphaFold prediction of D3: P52616[57,58]), (F) *Caulobacter crescentus* FljK (PDB ID: 6XKY[append. 60]), (G) *Sphingomonas sp. A1* FliC (PDB ID: 3K8W[66]), (H) *P. aeruginosa* FliC (PDB ID: 8SUG[append. 34]), (I) *Sinorhizobium meliloti* FlaA (PDB ID: 7SN9[31]), (J) *Blastopirellula retiformator* FliC giant flagellin (AlphaFold prediction A0A5C5VAD5[57,58]).

they grouped into 135 clusters.[33] The same study identified 52 and 26 hypervariable region forms in *E. coli* and *S. enterica*, respectively, none of which had significant sequence similarity with flagellins from any other species.[33] However, it is likely that the structural diversity of flagellin outer domains is much less than their sequence diversity since flagellin outer domains with no significant sequence similarities can share the same structure.[34]

Flagellin outer domains can also form dimers or tetramers between subunits to form complex outer-domain sheaths or screw-like structures (figure 7).[35] In *Sinorhizobium meliloti*, the outer domains form dimers resulting in three ridge structures that spiral around the filament, giving it a screw-like appearance (figure 7b).[35] *Achromobacter* and enteropathogenic *E. coli* O127:H6 flagellin outer domains form tetramers, resulting in mesh-like outer-domain sheaths (figure 7c, d).[35] The outer domains of enterohemorrhagic *Escherichia coli* O157:H7 flagellins dimerize to form a mesh-like outer-domain sheath (figure 7e).[35] Given the diversity in outer-domain sheaths known from the few species studied so far (described above), there is likely more outer-domain sheath diversity yet to be discovered.

Multiple 'giant flagellins' from diverse species have also been found that are over one thousand amino acids in length (about twice the size of typical flagellins), have giant outer domains, and form thicker filaments (figure 9j).[36,37] It is worth noting that the flagellins of most Firmicutes, including *B. subtilis*, and other species such as *Magnetococcus massalia* strain MO-1, do not have any outer domains (see the *C. crescentus* flagellin and filament, shown in figures 7f and 8a, respectively).[38,39] Flagellin varies greatly in size from 26 kDa (237 amino acids) in *Bacillus cereus* to 115 kDa (1128 aa) in *Desulfotalea psychrophila*.[38]

Glycosylation of flagellins is common in gram-negative species, including Enterobacteriaceae and Spirochaetota species, and is also present in some gram-positive species.[40–46] Flagellin glycosylation is most common in gram-negative pathogenic bacteria.[41] For example, the flagellins of *C. jejuni* and *H. pylori* are glycosylated with pseudaminic acid.[47] The flagellin of *C. jejuni* is one of the most heavily glycosylated proteins known, making up about 10% of its molecular weight.[47] This glycosylation is necessary for flagellar biosynthesis, without which the cell is non-motile.[47] Flagellar glycans serve many different roles, including in motility, virulence, flagellar assembly, and assembly of the *Leptospira* sheath (discussed below).[48–52]

Glycosylation is not the only way flagellins are modified. The flagellins of some species (e.g., *S. enterica*) are also methylated to improve adhesion and host-cell invasion.[53] Other flagellins are modified through phosphorylation.[54,55]

Around 45% of bacterial species contain two or more flagellin genes, including *H. pylori*, *C. crescentus*,

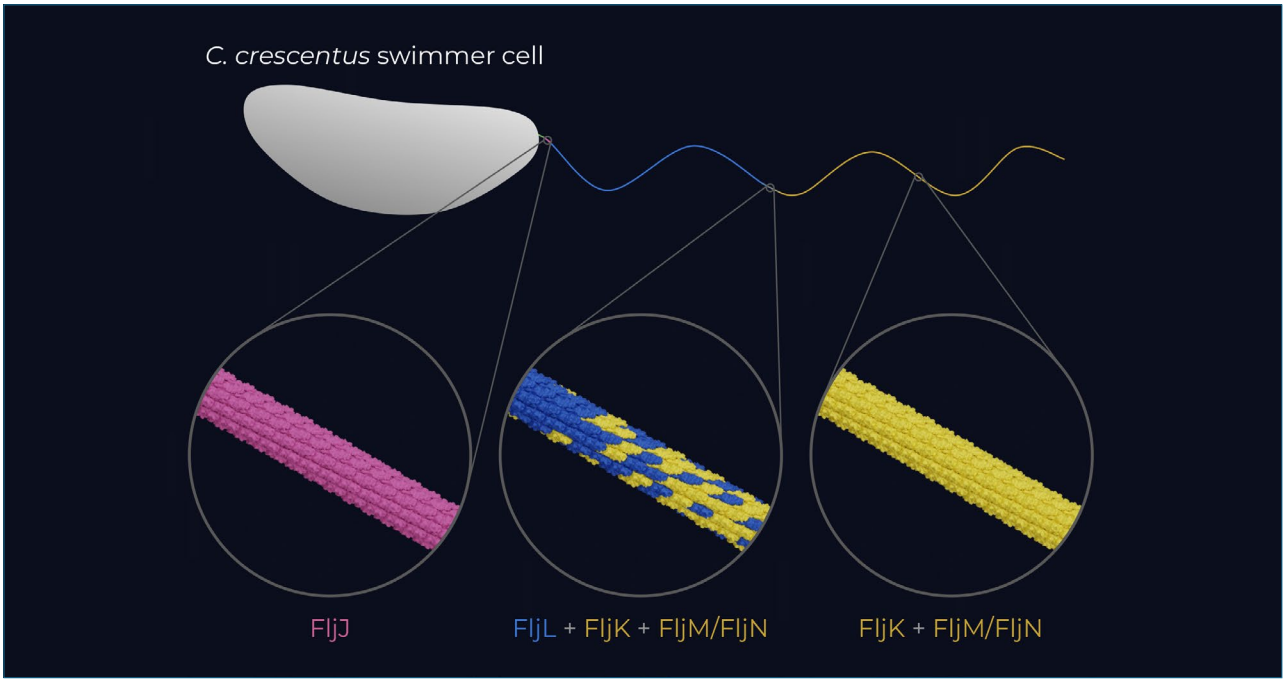


Figure 10. Flagellin abundance change along *C. crescentus* filament (PDB ID: 6XKY) based on data from appendices ref. 60. The first 60 nm contains the flagellin FljJ (shown in pink); the next 1 to 2 µm is made of the flagellin FljL (shown in blue) and increasing amounts of the flagellins FljK and FljM or FljN (shown in yellow), and the remaining 2 to 10 µm is made of the flagellins FljK and FljM or FljN (shown in yellow). Note, the precise arrangement and abundance of FljK, FljM, and FljN is not known. *C. crescentus* also codes for a flagellin called 'FljO', which was not detected in the filament and is expected to be present in low abundance.

Bdellovibrio bacteriovorus, *Sinorhizobium meliloti*, *Vibrio* species, and *Campylobacter* species.[38,56–58] For example, *C. crescentus* has six (possibly seven) and *V. cholerae* has five.[59–61] The *Magnetococcus marinus* strain MC-1 has 15.[59] The filaments in the closely related *Magnetococcus massalia* strain MO-1 are made of 12 flagellins, with two being more abundantly expressed.[62]

Typically, in species with multiple flagellin genes, the abundance of specific flagellins is different in the proximal end of the filament than in the middle and distal ends of the filament.[63,64] This difference in flagellin abundance causes the filament proximal end to have different mechanical properties than the rest of the filament. As a result, motility is improved in a range of environments, particularly by promoting screw-like motility (see part 3).[63] The filament of *C. crescentus* has three segments along its length, each with different quantities of various flagellins (figure 10).[65]

The polar and lateral flagella of *Shewanella putrefaciens* are each made of two flagellins. The proximal end of the polar flagellum is predominantly made of one flagellin while the rest is predominantly made of the other. Surprisingly, there is no such spatial arrangement of the flagellins in the lateral flagella.[66]

As mentioned in part 1, the two flagellin genes of *S. enterica* are not expressed at the same time, resulting in its flagella being made of only FliC or only FljB at any given time.[67] This switching is used to evade the host's immune response.

Spirochetes' filaments are typically made of multiple flagellins, with FlaB flagellins forming the core of the filament and FlaA flagellins binding around the FlaB core (figure 11).[68] The number of FlaA and FlaB flagellins differs among spirochete species. For example, *Brachyspira* and *Treponema* species have three FlaBs and one FlaA, *B. burgdorferi* has one of each, and *Leptospira* has at least one FlaB and two FlaAs.[68,69] *Leptospira* also has two *Leptospira*-specific flagellar filament proteins, FcpA and FcpB.[70] The *Leptospira biflexa* sheath is very complex and asymmetrical, with the outer, convex side of the filament being coated in an interlocking array of six rows of FcpA and four rows of FcpB (figure 11).[71] The concave side of the filament has two rows of proteins, one made of FlaAP, FlaA2, and an unidentified protein, and the other made of an unidentified protein (figure 11).[49,71] A groove (gap in the sheath) lies between these two rows. This asymmetric sheath promotes the tight supercoil geometry of the *L. biflexa* filament, which is important for *Leptospira* motility.[49,71]

Flagellins can be more than structural proteins. At least 74 bacterial species have flagellins that form enzymatically active filaments and can cleave nearly 1,000 different peptides.[32,72]

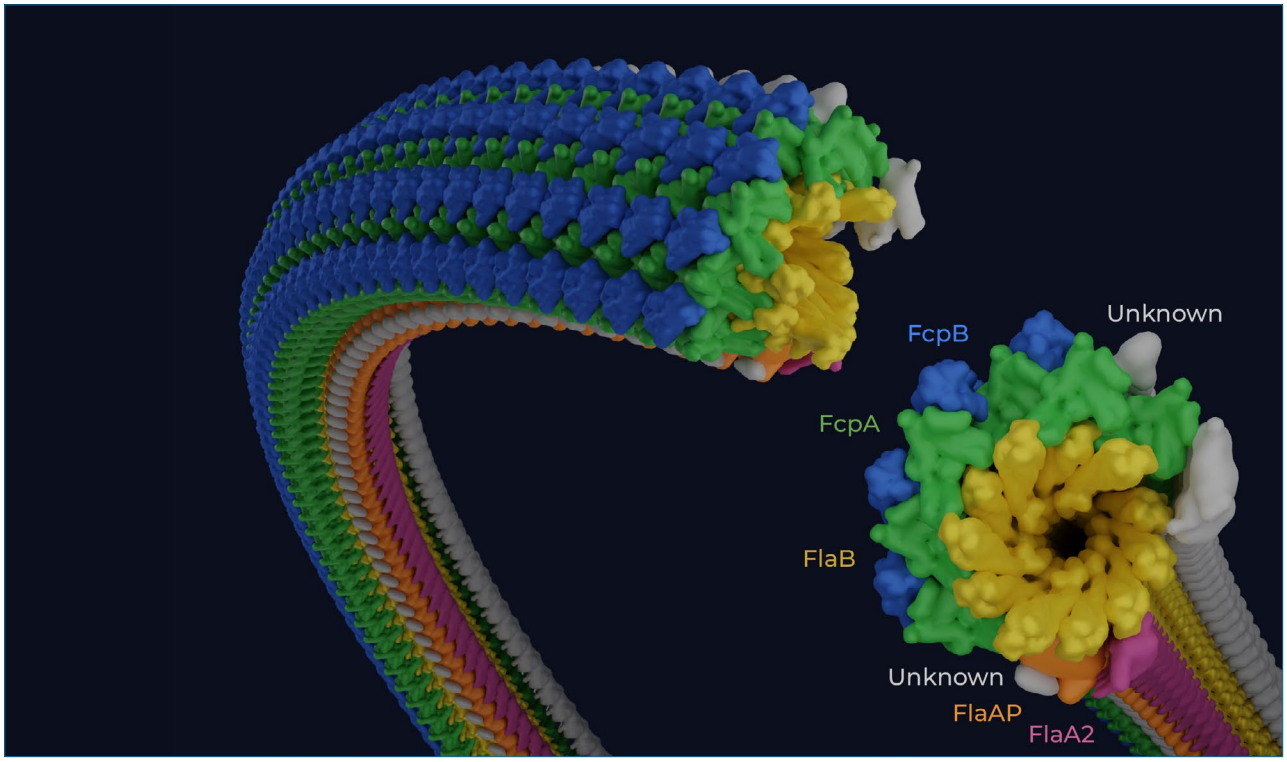


Figure 11. *Leptospira biflexa* flagellar filament proteinaceous sheath (based on PDB ID: 6PWB[append. 71]) viewed from two different angles. Filament (formed by FlaB) shown in yellow. Sheath (formed by multiple different proteins) shown in green, blue, orange, pink, and white.

Appendix 2

The flagellar motors of many species, especially high-torque polar and periplasmic flagellar motors, have cage, ring, and/or disk structures around them for structural support.[73,74] A few of the proteins that make up these structures have been identified, including FlgO, FlgP, FlgT, MotX, and MotY in *Vibrio* species, PflA and PflB in ε-proteobacteria, and FlbB, FlcA, FlcB, FlcC, FlgV in Spirochetes, but the identities of many other proteins remain to be discovered.[1,19,74–77]

Vibrio species are abundant in aqueous environments and have a single polar flagellum that is typically encased in a membranous sheath.[78] Their flagellar motors have a stator-stabilizing scaffold to hold their 13 sodium-powered PomAB stators (figure 12). This scaffold is made of two rings called the 'H-ring' and 'T-ring'.[1,17] The H-ring is made of the lipoproteins FlgO and FlgP and the periplasmic protein FlgT.[19,19] The T-ring is made of MotX and MotY.[1] These stabilizing structures allow the motor to spin at far higher speeds than enteric motors (up to 102,000 rpm).[79] A ring called the 'O-ring' surrounds the base of the membranous sheath, which is likely important during sheath construction.[1]

The single polar flagellar motor of *C. crescentus* contains additional parts called the 'cog wheel' (named after its shape, not function) and the OM-ring (figure 13).[80] The function of the additional parts is not yet known. However, the OM-ring has a similar location to the Yec-R ring described in part 1 and the cogwheel appears to function as an attachment to the cell wall. The motor is optimized for speed and efficiency rather than thrust, well-suited to its low-nutrient, low-viscosity, freshwater environment.[81] Additional thrust is produced by the helical motion of the helical-crescent-shaped cell body (figure 10).[19]

C. jejuni's two bipolar flagellar motors have three large disk structures (figure 14); namely, the basal disk (made of FlgP), the proximal disk (made of PflB), and the medial disk (made of PflA and possibly FlgQ).[82,1,73] The basal disk has 11-fold rotational symmetry.[83] These disks hold 17 MotAB stators around the motor.[17]

Each of *H. pylori's* polar flagellar motors have a wide central gear driven by 18 powered gears held within a large

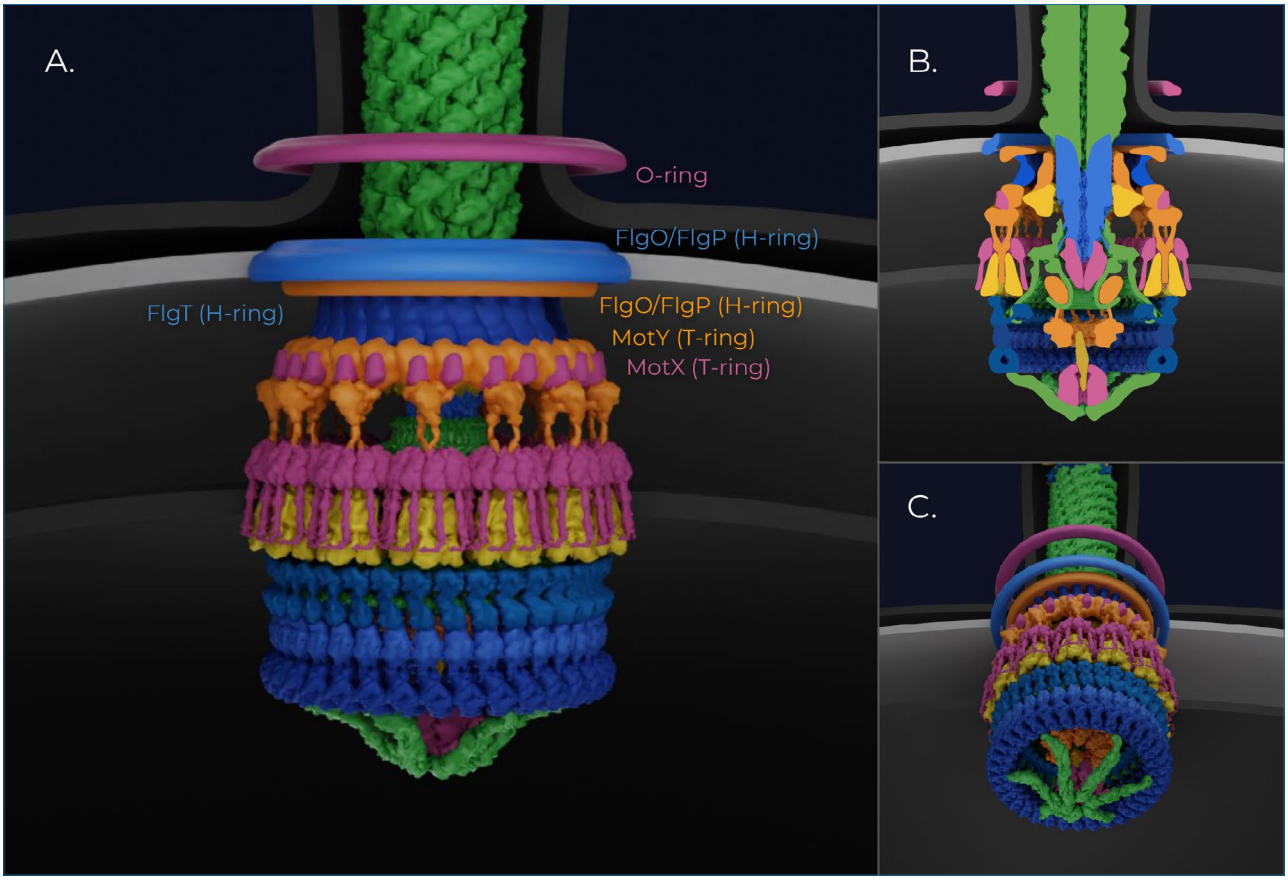


Figure 12. *V. alginolyticus* motor (based in part on EMD-21027[66]). (A) Front view, (B) cross-section diagram, (C) low view.

cage-like structure with 18-fold rotational symmetry (made of PflA and PflB, the type IV pili proteins PilO, PilN, and PilM, and at least one unidentified protein) (figure 15).[82,74,84–86] Nestled within the cage structure around each stator is a FliL ring, a structure likely present in all flagellated bacteria.[84,87] Around the base of the hub-central gear junction is a ring made of FlgV, a structure likely present in other species of the phylum Campylobacterota (e.g., *C. jejuni*) to stabilize this critical junction (figure 15b, c).[88] FlgV, or FlgV-like proteins, are also present in some spirochetes, firmicutes, the PVC clade, and *Arcobacter*-like epsilonproteobacteria.[77] The motor also has two large disk structures below the outer membrane, one of which appears to be made of concentric rings of FlgP and potentially other proteins.[74] A similar distal disk showing concentric rings with a maximum diameter of 90 nm has been observed in the β-proteobacterium, *Aquaspirillum serpens*.[89,90] The *H. pylori* motor generates a lot of torque (around 3,600 pN·nm), allowing *H. pylori* to swim through highly viscous fluids.[17]

Other polar flagellar motors are illustrated in figures 16 to 20. That of *Wolinella succinogenes* also has a cage structure like *H. pylori*, though the cage has 17-fold rotational symmetry instead of 18-fold and has a slightly different shape (figure 16).[74] The distal portion of the flagellar motor has a design more similar to the *C. jejuni* motor.[74] The motor of *Arcobacter butzeri* has multiple ring structures (made of PflA, PflB, and other proteins) with 16-fold rotational symmetry and a disk just below the outer membrane with five concentric grooves (figure 17).[74] The motor of *B. bacteriovorus* has a ring structure with 12-fold rotational symmetry (made of PflA), a modified L-ring design, and a sheathed flagellar filament (figure 18).[74] *Helicobacter hepaticus* has a motor with multiple ring and disk structures (made of proteins including PflA and PflB) and a sheathed flagellar filament (figure 19).[16] Each of the polar flagellar motors of *Hylemonella gracilis* contain a disk above the stator ring (figure 20).[16]

Spirochete flagellar motors are surrounded by a unique and very complex 'collar' structure (figures 21–23).[91–94] The collar is made of multiple proteins: in *B. burgdorferi*, FlcA forms the outermost portion and binds to the cell wall; FlbB forms a ring structure at the base of the collar; FlcC forms the

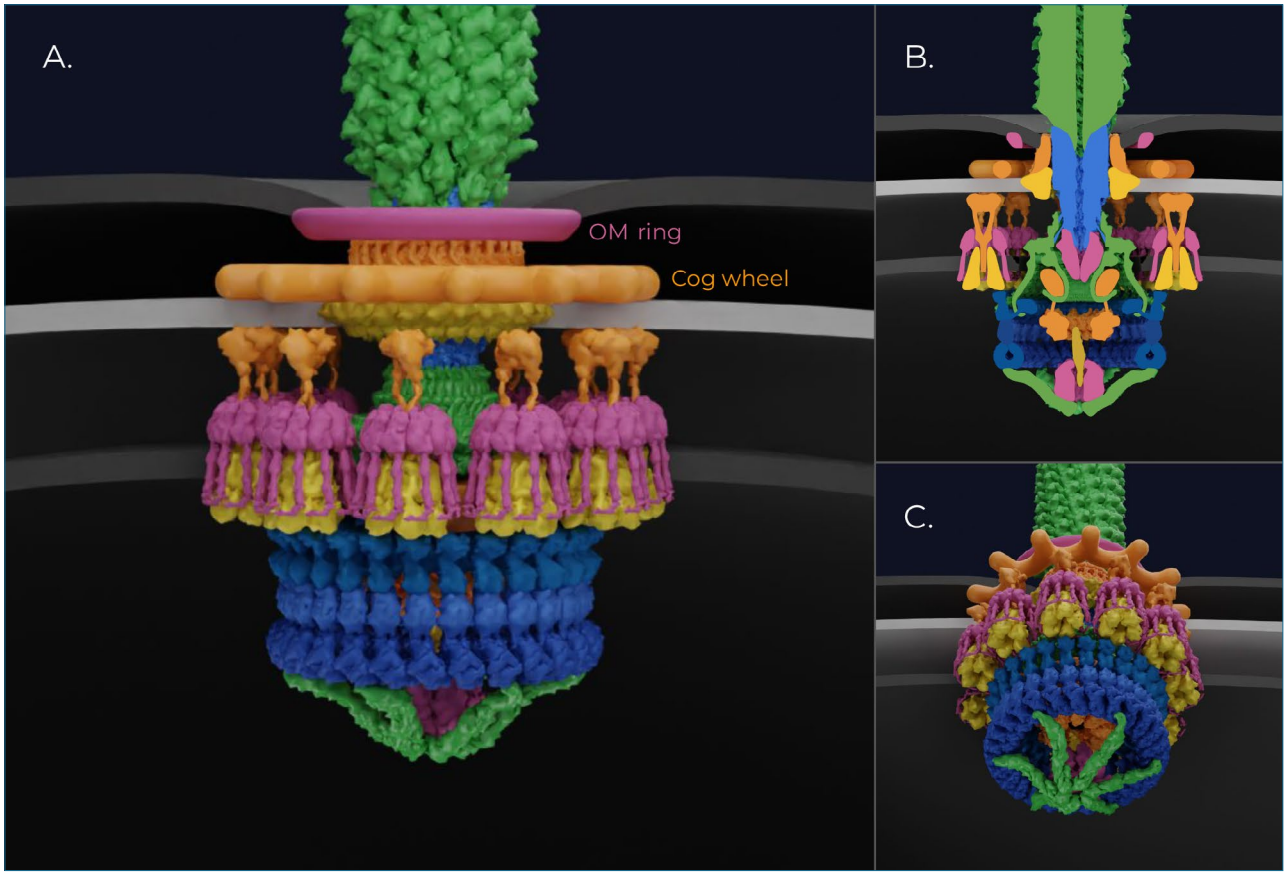


Figure 13. *C. crescentus* motor (based in part on figure 2 of appendices ref. 80). Hook structure based on AlphaFold prediction P35806.[57,58] (A) Front view, (B) cross-section diagram, (C) low view.

top part of the collar; and FlcB forms a ring in the innermost part of the collar (figure 22).[91,39,75,76] Surprisingly, most of these collar proteins are not found in other spirochetes, such as *Leptospira* species, *Treponema* species, and *Brachyspira* species, indicating that the collar structure in these species must be formed from different proteins (figure 23).[95]

Nestled within the collar structure around each stator is a FliL ring.[85] Spirochete motors can produce torque as high as 4,000 pN·nm, making them one of the most powerful known flagellar motors in the bacterial domain.[96,97] This high torque is necessary to rotate the filaments within the periplasm and drive the cell body through highly viscous media.[25]

The most studied spirochete flagellar motor is that of *B. burgdorferi*, the causative agent of Lyme disease.[98] It has a large central gear (62 nm in diameter) and 16 powered gears, which are held in a collar structure with 16-fold rotational symmetry (figures 21 and 22). The collar is reinforced with internal triangular truss-like structures.[93] The collar and powered gears are curved to match the curvature of the inner membrane of the cell (not shown in figures 21 and 22).[91,93] To maintain alignment between the central gear and the powered gears, the central gear has to flex as it rotates.[93] The attachments between the central gear and the hub likely function as ball joints to accommodate this flexibility.[93]

The seven motors in the hexagonal flagellar motor array of *Magnetococcus massalia* MO-1 are embedded in a large, thick bowl-shaped disk structure called the 'base-platform', which is likely made of the outer-membrane, peptidoglycan layer, and various proteins (figure 6).[99] The filament sheath, which is made of glycoproteins, also attaches to the base-platform.[99] The filament bundle contains 24 thin fibrils (shown in orange in figure 6), which have a smooth appearance and likely act as bearings between the filaments to reduce friction.[99] The fibrils appear to fit into small ring structures embedded in the base-platform (shown in yellow in figure 6).[99] The magnetotactic cocci with the 3:4:5:4:3 motor array appear to have a similar base-platform assembly around 400 nm across.[100]

Many species also have parts, such as brakes or clutches, which are only present at specific times. These will be discussed in part 4.

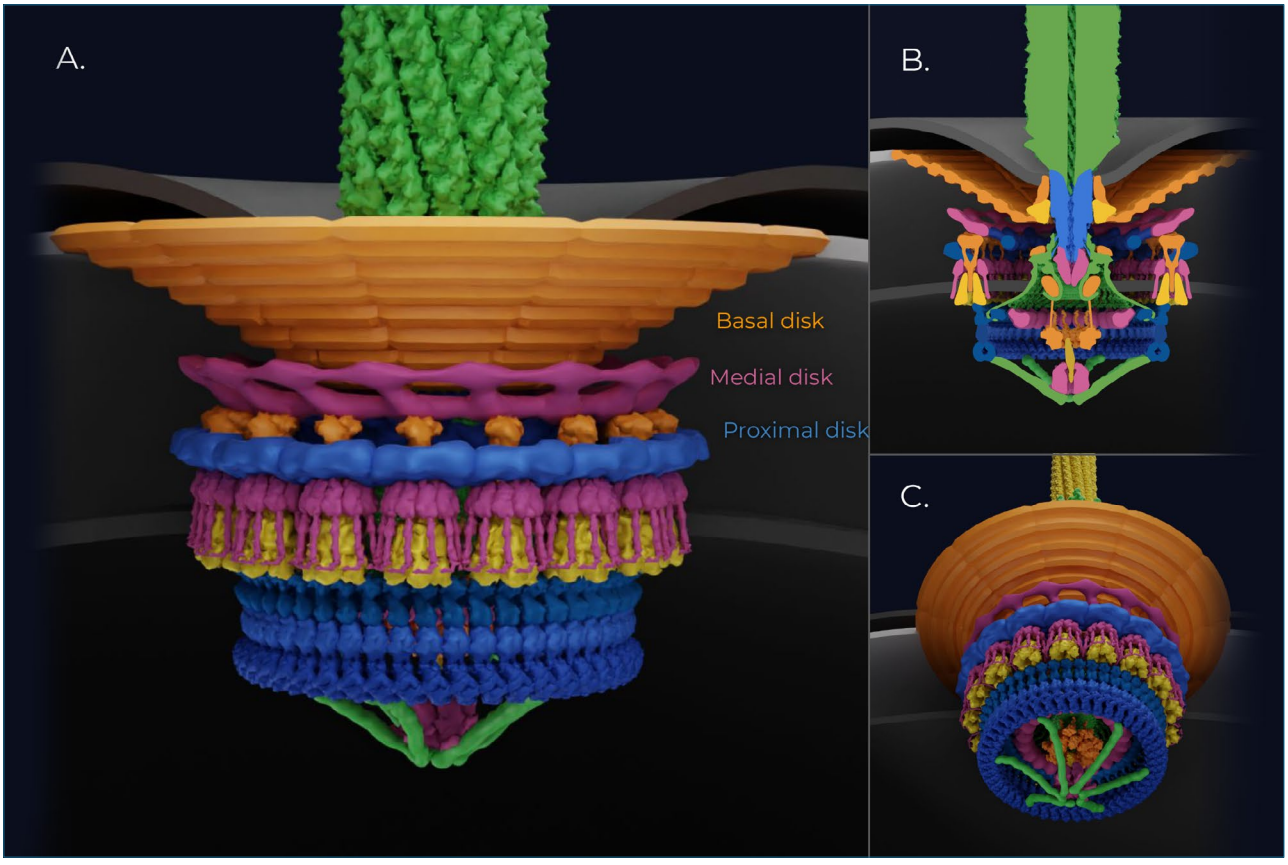


Figure 14. *C. jejuni* motor (based in part on EMD-3150[append. 17]). Central gear protein FliY not shown. Basal disk shown in orange, medial disk shown in pink, and proximal disk shown in blue around the top of the stator ring. The inner part of the medial disk, made of PflA, and the proximal disk, made of PflB, are both coloured blue to match the colouring in other figures. The outer part of the medial disk, shown in pink, may be made of FlgQ. (A) Front view, (B) cross-section diagram, (C) low view.

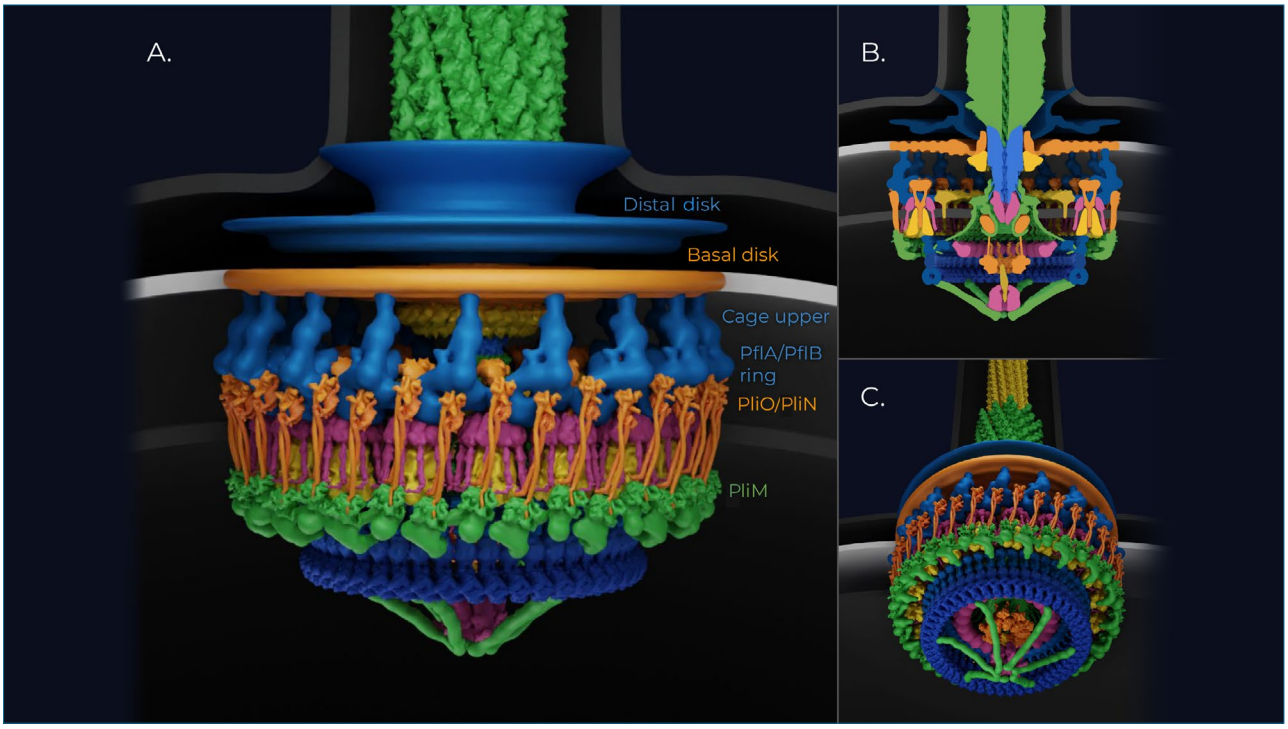


Figure 15. *H. pylori* motor (based in part on EMD-25123,[append. 84] EMD-40405,[append. 86] EMD-40406[append. 86] and PDB ID: 3JC8). Central gear protein FliY not shown. (A) Front view, (B) cross-section diagram; note the FlgV ring (pink) inside the central gear, (C) low view.

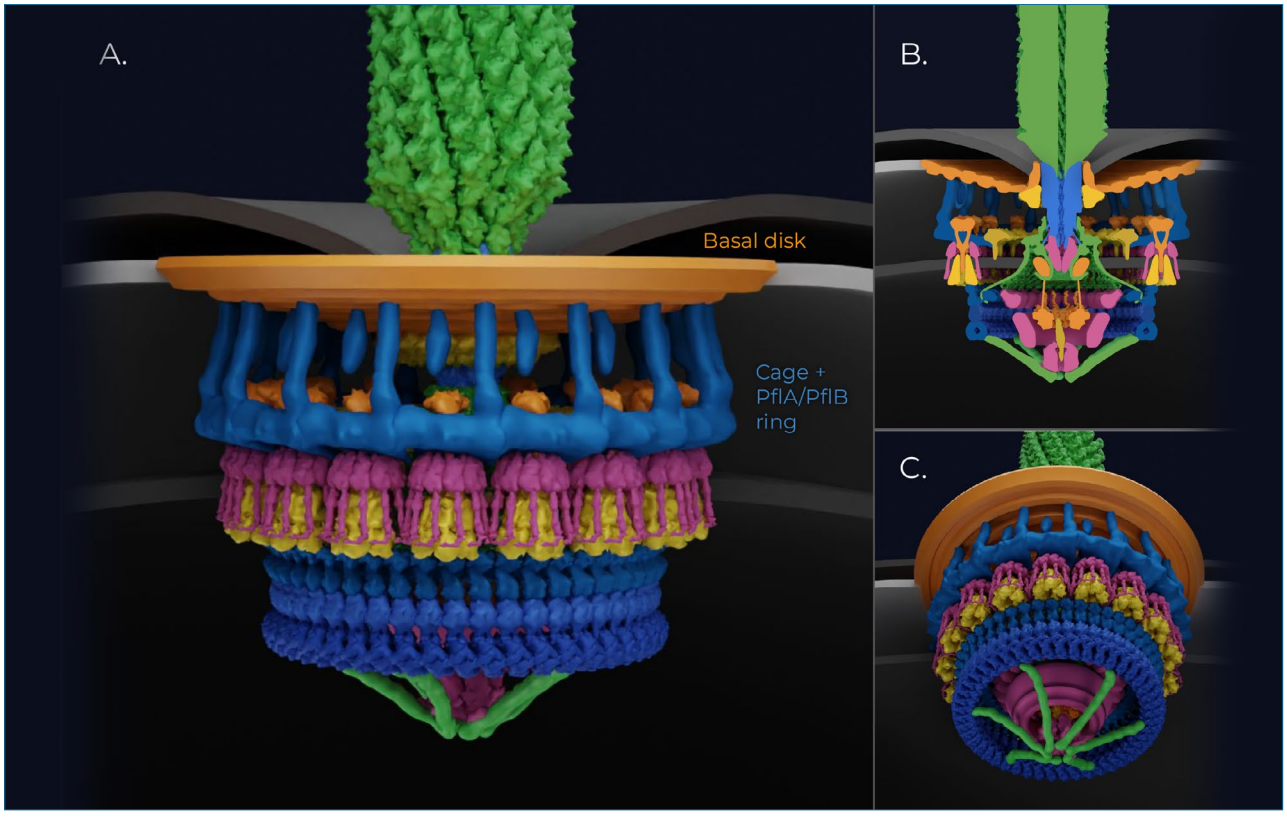


Figure 16. *W. succinogenes* motor (based, in part, on EMD-3912[54]). (A) Front view, (B) cross-section diagram, (C) low view.

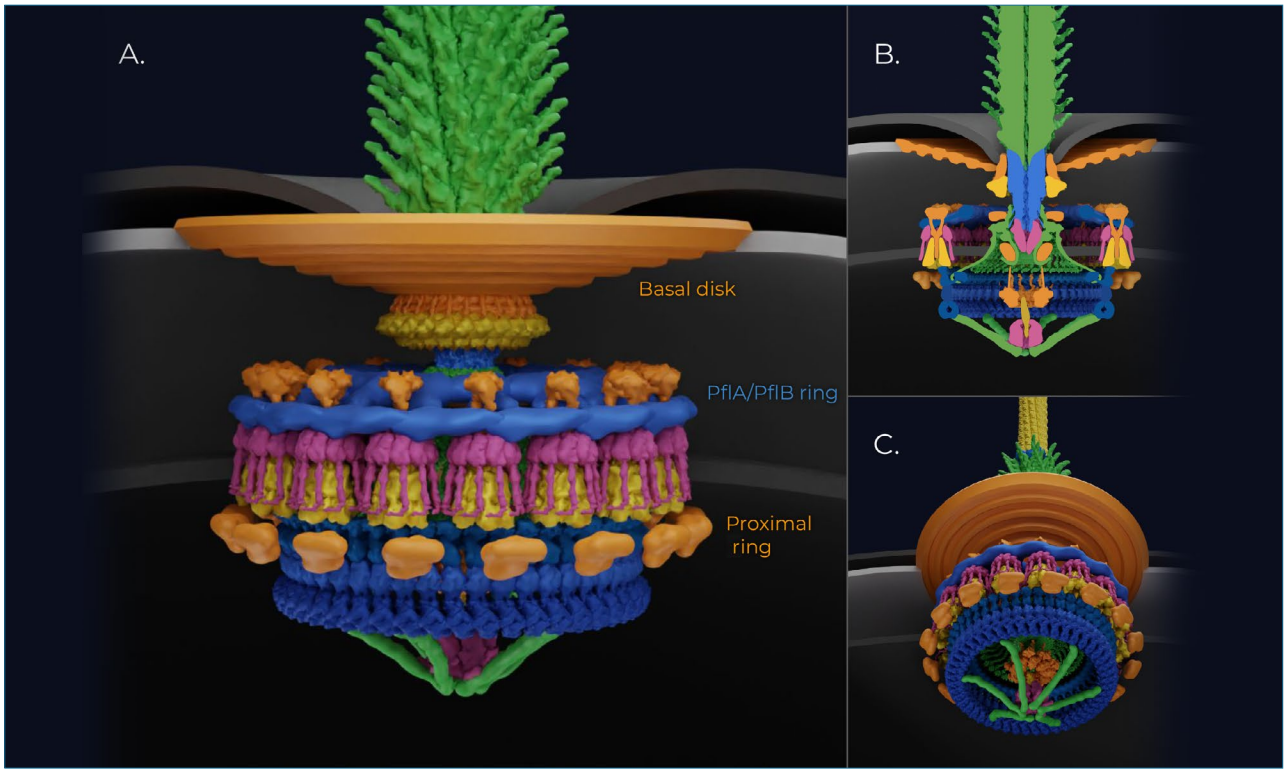


Figure 17. *A. butzeri* motor (based, in part, on EMD-3910.[54] Hook structure based on AlphaFold prediction A8EW57[57,58]). (A) Front view, (B) cross-section diagram, (C) low view.

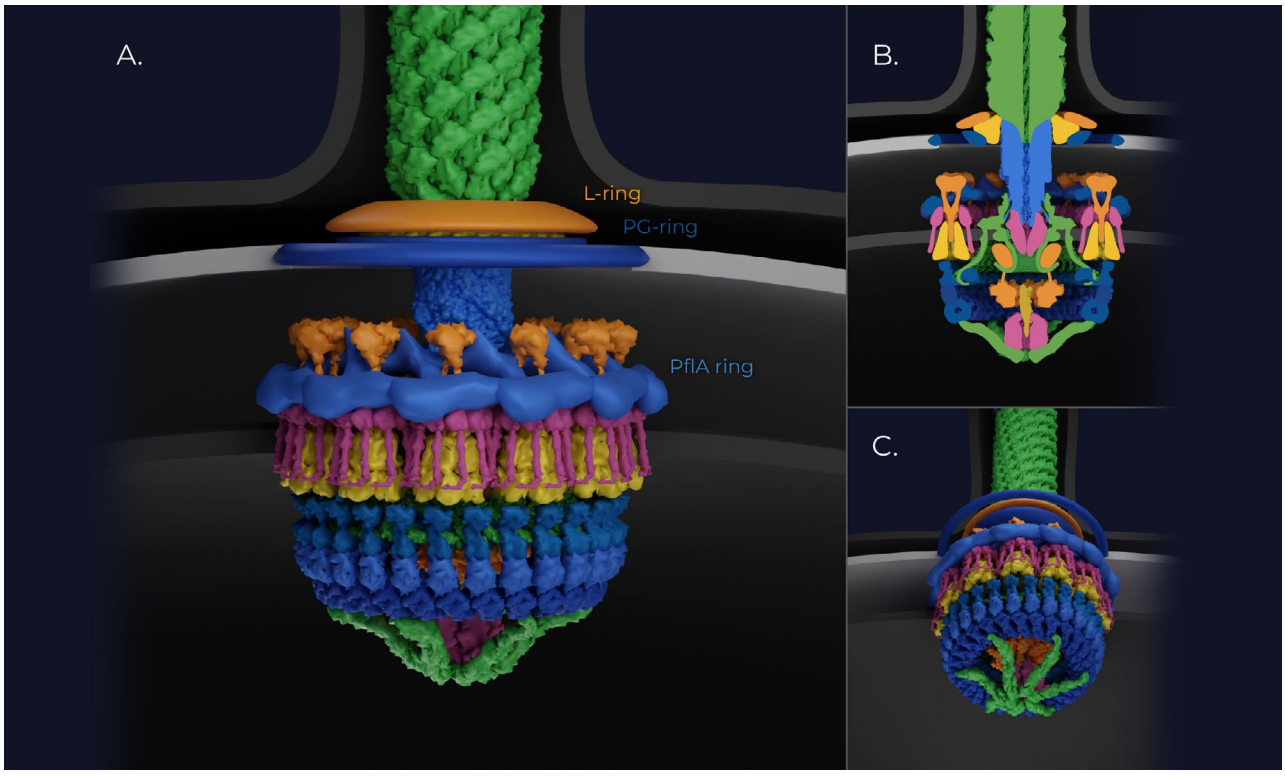


Figure 18. *B. bacteriovorus* motor (based, in part, on EMD-3911[54]). (A) Front view, (B) cross-section diagram, (C) low view.

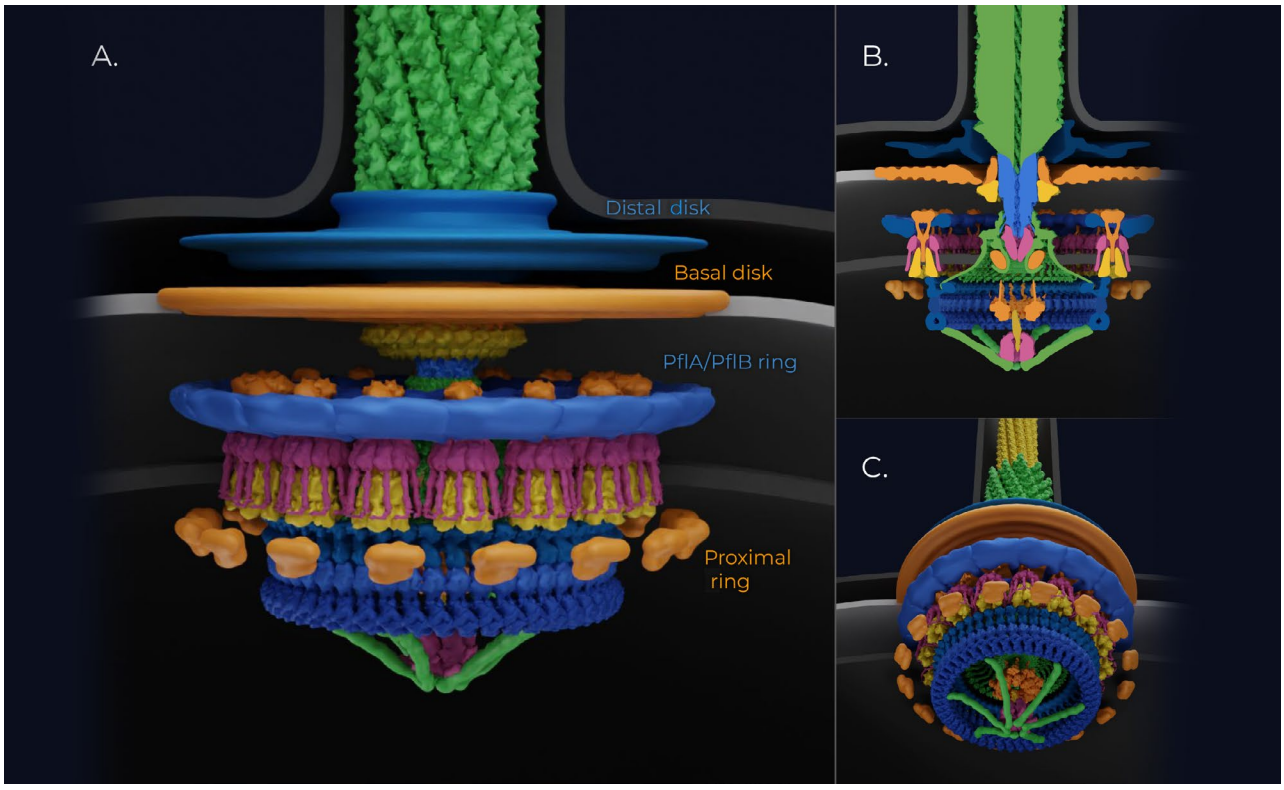


Figure 19. *H. hepaticus* motor (based, in part, on EMD-5299[36]). (A) Front view, (B) cross-section diagram, (C) low view.

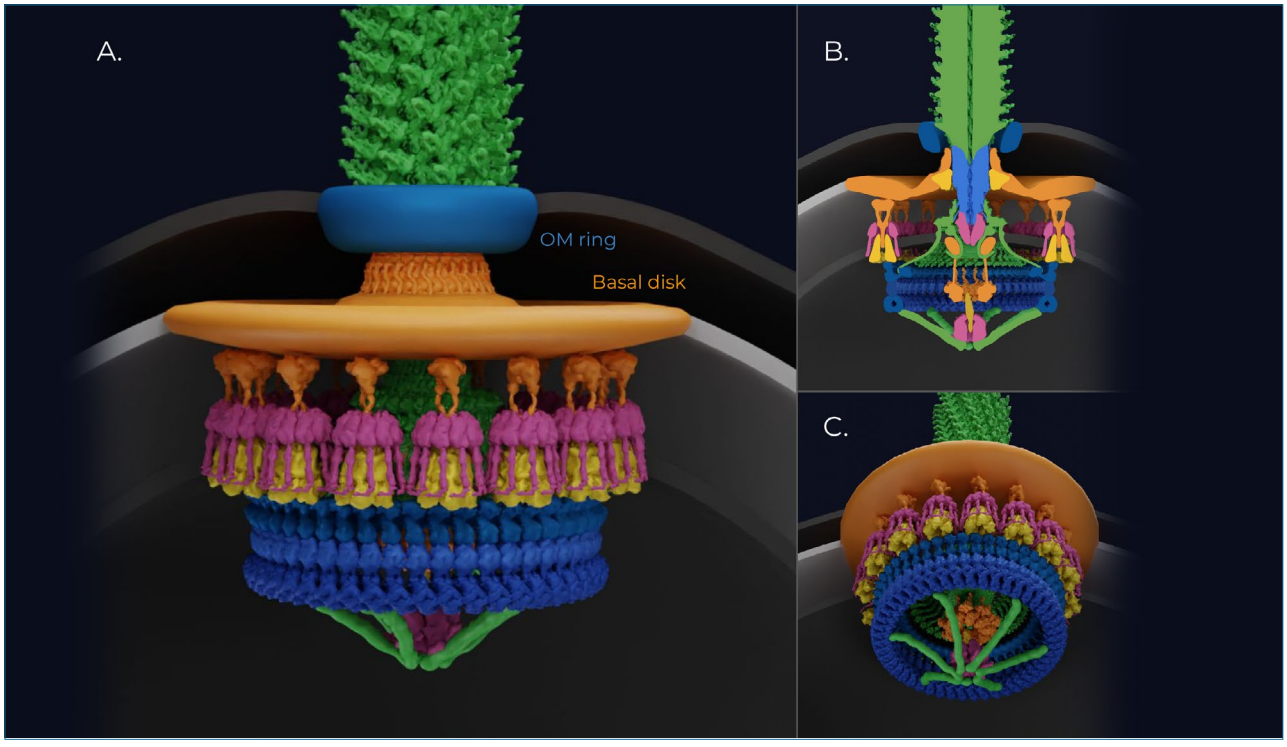


Figure 20. *H. gracilis* motor (based in part on EMD-5309.[36] Hook structure based on AlphaFold prediction F3KXY5[57,58]). (A) Front view, (B) cross-section diagram, (C) low view.

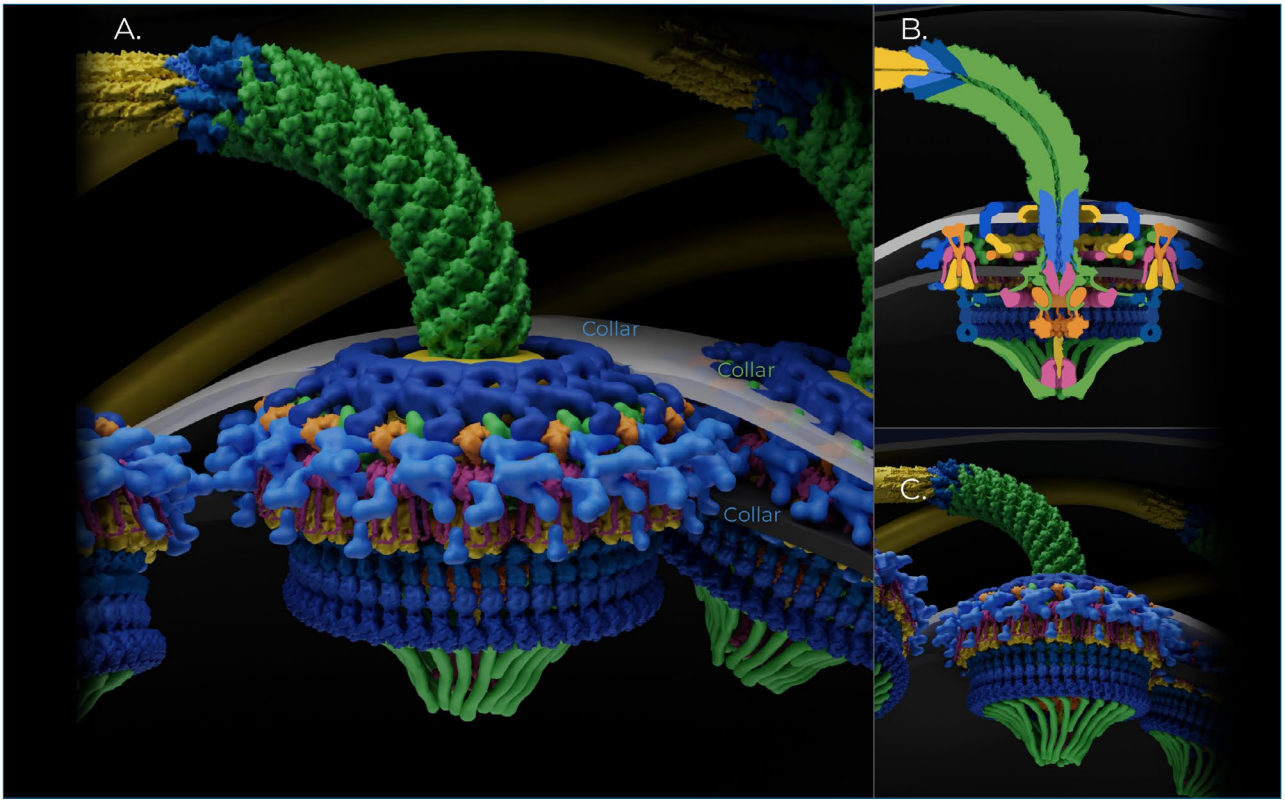


Figure 21. *B. burgdorferi* flagellar motor (based, in part, on EMD-0536[append. 93]). (A) Front view, (B) cross-section diagram, (C) low view.

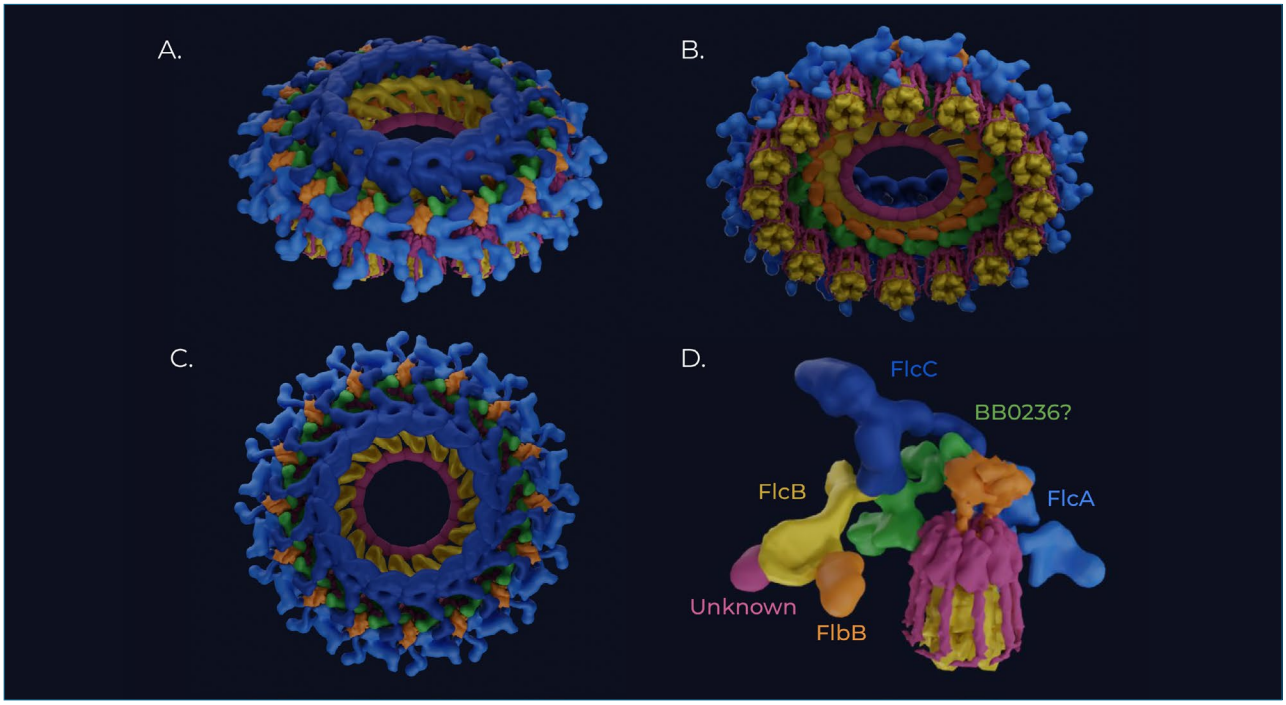


Figure 22. *B. burgdorferi* collar with stators (based, in part, on EMD-0536 and figure 5 of ref. 19). (A) High view, (B) low view, (C) top view, (D) the repeated unit of the collar with one stator complex. The protein shown in green is likely BB0236, since the shape of this density matches the AlphaFold prediction of BB0236,[57,58] and BB0236 is known to directly interact with FlbB.

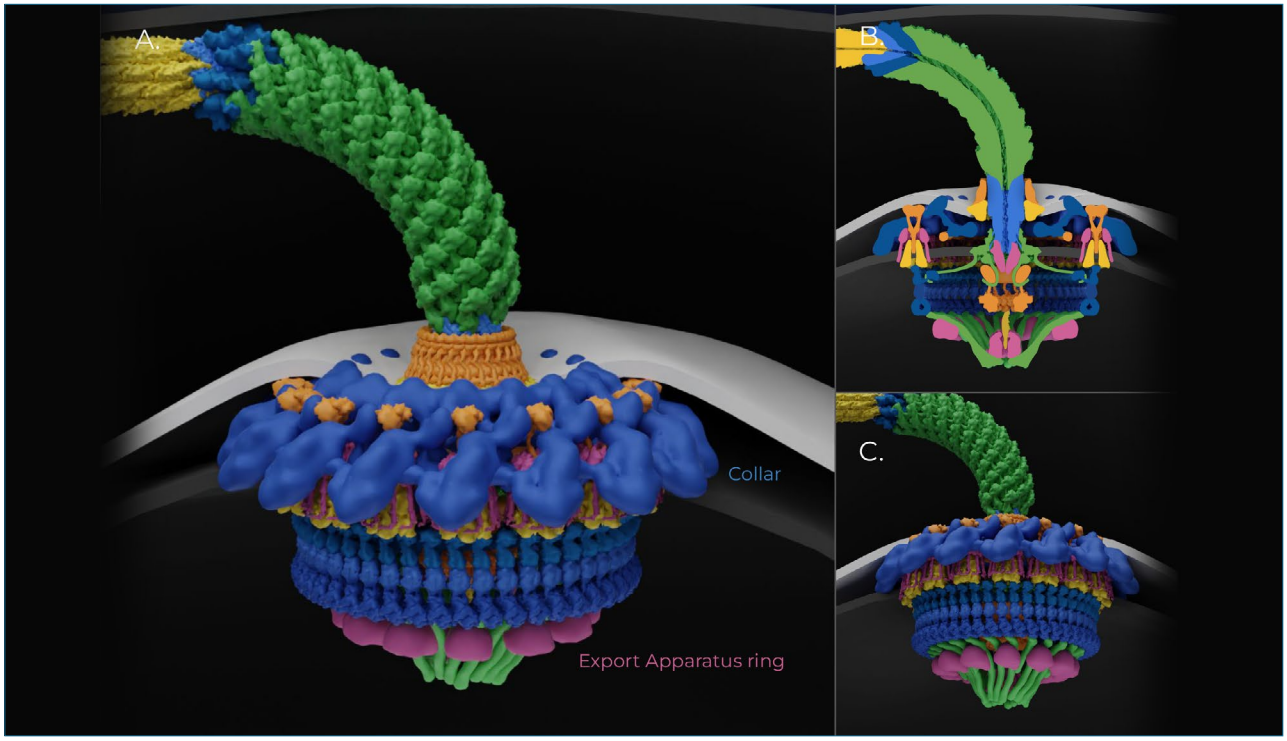


Figure 23. *L. interrogans* flagellar motor (based, in part, on EMD-5913[67] and EMD-5914[67]). *Leptospira* species, including *L. interrogans*, do not have the genes for the collar proteins FlcA, FlcB, FlcC, or BB0236 (but do have FlbB). Therefore, the collar in *Leptospira* species must be made of different proteins to those found in *B. burgdorferi*. (A) Front view, (B) cross-section diagram, (C) low view.

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