The design of bacterial flagella: part 2—flagellar diversity across bacterial species

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As expected from a design perspective, bacterial flagella show significant diversity in their design across the bacterial domain. Flagella differ between species in five main ways: (1) the number and arrangement of flagella per cell, (2) the presence of sheaths surrounding flagellar filaments, (3) the structure of the parts found in all flagella, (4) the structure of additional parts found in the flagella of only some species, and (5) their function (what flagella are used for). This paper is the second in a seven-part review on the design of bacterial flagella and their associated systems. The structural design of the flagella of the model organisms *Escherichia coli* and *Salmonella enterica* was discussed in part 1. In this paper, the flagellar designs observed in other bacterial species are shown to differ significantly from those found in the model organisms.

Pioneering research on the structure of bacterial flagella, from various species, used purification techniques that removed many flagellar parts from the flagellar structure when isolating them from cells. The parts that remained (such as the MS-ring, rod, hook, and filament) appeared very similar among species.[1] This gave the false impression that flagella have a very similar structural design across the bacterial domain.[1] In reality, flagellar structural design is diverse with most flagella containing additional parts not found in the flagella of the model organisms discussed in part 1 (*E. coli* and *S. enterica*)[2] (figure 1).

Over 80% of bacterial species have flagella.[3] The distribution of flagella across the domain Bacteria does not match what would be expected from a Darwinian tree of common descent (see part 7).[4] Evolutionists have argued that the diversity of flagellar designs across the domain Bacteria is evidence against design because, from their perspective, a Designer would not make diverse designs.[5,6] However, this is a theological argument, not a scientific one, and breaks down when human design approaches are considered.[4] Humans frequently design things with considerable diversity, especially when product variants need to be optimally designed to satisfy various constrains (e.g., a city car vs an off-road car vs a race car). Flagellated bacteria live in diverse environments and have different lifestyles, both of which impose design constraints in order to optimize flagellum function. With these things in mind, we *would* expect to see much diversity in the design of bacterial flagella. And indeed we do. The design of flagella differ among species in five main ways:

1. the number and arrangement of flagella per cell
2. the presence of sheaths surrounding flagellar filaments
3. the structure of the parts common to all flagella
4. the structure of additional parts found in the flagella of only some species
5. the function of flagella.

Each of these areas of diversity is discussed below.

1. The number and arrangement of flagella per cell

The clearest difference in flagella systems among bacterial species is the number and arrangement of flagella. There are at least nine different bacterial flagellar arrangements (table 1, figure 2) and these can significantly affect swimming behaviour, as will be discussed in part 3.

Flagella can be organized broadly into three systems—polar (at the cell pole(s)), lateral (along the side of the cell body), and peritrichous (evenly covering the cell body).[7] Polar is likely the most common flagellar system, especially in marine environments, where 90% of motile bacteria have a single polar flagellum (monotrichous).[8,9] The flagella of different systems have distinct morphologies suited to different environments and swimming behaviours (see part 3).[7] Polar flagella typically have a pitch and diameter half that of peritrichous flagella.[7]

Several examples of flagellar arrangements in various bacterial species will be mentioned, commencing with two examples of bacteria with polar flagella. *Spirillum volutans* has a bundle of about 75 external flagella at each pole.[10] In contrast, *Campylobacter jejuni* has just one flagellum at each pole.[11] Both *S. volutans* and *C. jejuni* have helical cell bodies like spirochetes, which allows them to produce some thrust from rotation of their bodies.[10]

Vibrio species possess two flagellar systems. They have a lateral flagellar system (used for swarming motility on surfaces) and a polar flagellar system (used for swimming

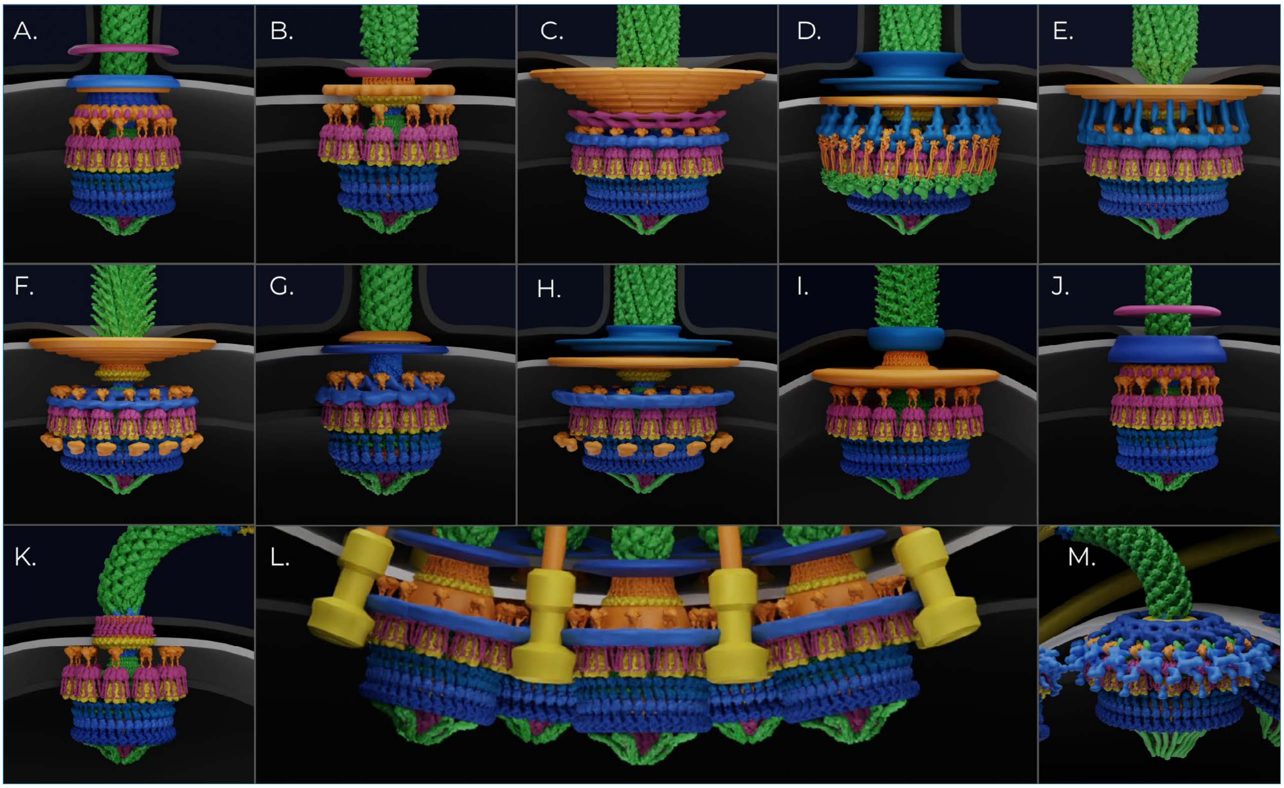

Figure 1. Computer models of a selection of diverse flagellar motor designs, based, in part, on Cryo-EM data, RCSB Protein Data Bank files,[59] and AlphaFold predictions.[60,61] (A) *V. alginolyticus,* (B) *C. crescentus*, (C) *C. jejuni*, (D) *H. pylori*, (E) *W. succinogenes*, (F) *A. butzeri*, (G) *B. bacteriovorus*, (H) *H. hepaticus*, (I) *H. gracilis,* (J) *Shewanella oneidensis* (based, in part, on EMD-0467[62]), (K) *E. coli*, (L) *Magnetococcus massalia* strain MO-1, with two motors from the array removed, (M) *B. burgdorferi*.
Note: The central gears of *C. jejuni* and *H. pylori* contain a protein called 'FliY', which is not shown in these illustrations. Images not at same scale. Unless stated otherwise, computer models in figures were made in Blender 3.5 (blender.org) with the Molecular Nodes add-on (bradyajohnston.github.io/MolecularNodes).

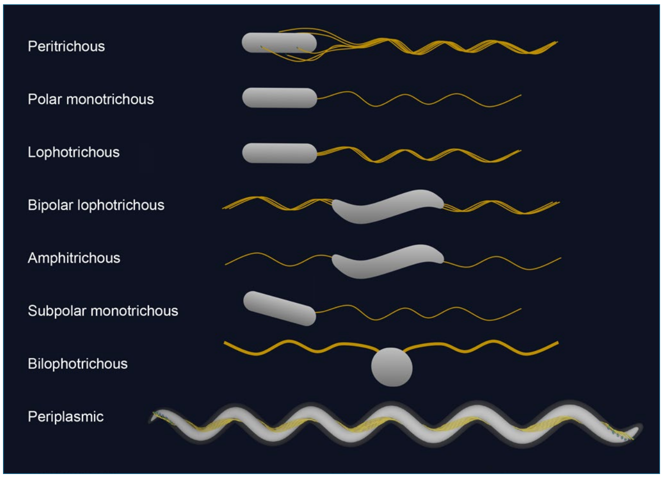

Figure 2. Flagellar arrangements. 'Periplasmic flagella', while not typically described as a flagellar arrangement, is included for comparison. Flagella shown in yellow. Cell bodies shown in grey (except for the spirochete cell body, where the PG-layer is shown in grey and the membranes are shown in transparent dark grey). The thick yellow lines of the bilophotrichous coccus cell represent bundles of seven or more flagella which are encased in a sheath.

motility in liquids).[12,13] The polar flagella are always expressed, but the lateral flagella are only expressed in viscous environments or on surfaces (see part 5 for how this is controlled).[12]

The spirochetes are bacteria characterized by a distinct flat-wave or corkscrew cell morphology—caused by unique subpolar intracellular flagella within the periplasm (figure 3).[14,15] Spirochetes have one or more periplasmic flagella (sometimes called 'endoflagella'), which extend from the cell poles in a parallel, ribbon-like arrangement and spiral around the cell body towards the cell centre (figure 3).[14,16,17] In the figure, it is evident that the motors at each polar location are arranged in a row that spirals away from the cell tip. Unlike species with external flagella that swim by pushing on the surrounding fluid with their flagella, spirochetes swim by the rolling or the undulation of the cell body as controlled by its endoflagella.[14,18] The genera of spirochetes vary widely in cell morphology, the number of flagella and whether their flagella overlap in the centre.[19] For example,

Table 1. Various flagellar arrangements observed in bacterial species

Name	Description	Example species
Peritrichous	Multiple flagella located uniformly across the cell body	*Escherichia coli, Salmonella enterica, Bacillus subtilis*
Polar monotrichous	A single flagellum at one pole	*Pseudomonas aeruginosa, Vibrio parahaemolyticus, Caulobacter crescentus, Bdellovibrio bacteriovorus, Shewanella oneidensis*
Lophotrichous	Multiple flagella located at one pole	*Helicobacter pylori, Pseudomonas fluorescens, Vibrio fischeri, Aquaspirillum serpens*
Bipolar lophotrichous	Multiple flagella located at both poles	*Spirillum volutans, Helicobacter suis*
Amphitrichous	A single flagellum at each pole	*Campylobacter jejuni, Magnetospirillum magneticum, Rhodospirillum rubrum*
Bilophotrichous	Two bundles of flagella on one cell hemisphere	*Magnetococcus massalia* strain MO-1, *Magnetococcus marinus* strain MC-1
Subpolar/medial monotrichous	A single flagellum near one pole or located mid-cell	*Cereibacter sphaeroides*
Lateral*	Multiple flagella along the sides of the cell body	*Vibrio parahaemolyticus, Azospirillum brasilense*
Periplasmic**	One or more periplasmic flagella extending from each pole and remaining within the periplasmic space	All spirochete species including *Borrelia burgdorferi, Leptospira biflexa, Treponema pallidum*

*Lateral flagella can exist in combination with other arrangements (e.g., polar monotrichous)

**Typically not described as a flagellar arrangement since it can fit under bipolar lophotrichous/amphitrichous

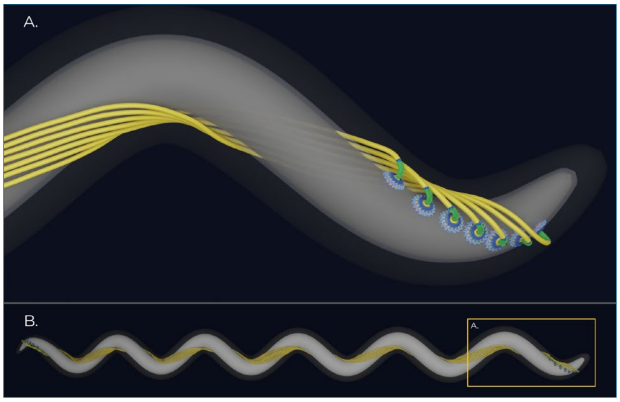

Figure 3. Periplasmic flagella of *B. burgdorferi* (membranes in transparent dark grey, peptidoglycan layer in transparent light grey). (A) Close-up of cell tip, showing motors spiralling around the cell body in a row and filaments forming a 'ribbon' that wraps around the cell body. (B) View showing whole cell body.

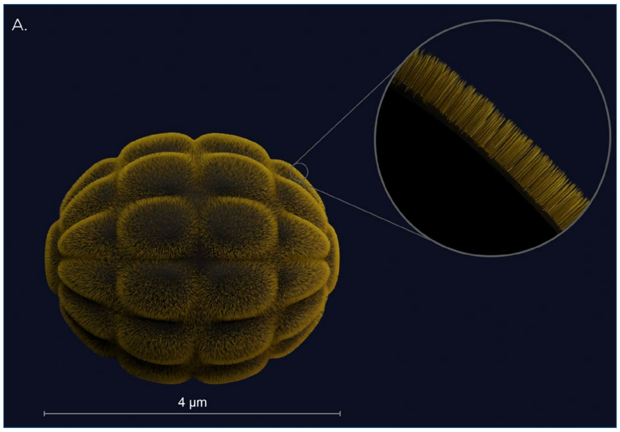

Figure 4. A model of an ellipsoidal bundle of multicellular magnetotactic prokaryotes (MMPs). Thousands of flagella form a fur-like coating over the surface of the bundle, similar to cilia. Inset shows close-up of flagella on cell surface.

Borrelia burgdorferi has a flat-wave morphology and has seven to eleven flagella at each pole that overlap in the centre (figure 3). In contrast, *Leptospira illini* has a corkscrew morphology and one flagellum at each pole, which do not overlap.[12,14,20] There are also some large spirochetes with hundreds of endoflagella,[21] which undoubtedly means added complexity is involved.

In ovoid bacteria that orientate along magnetic field lines (magnetotactic), a more refined classification version of flagellar arrangements (table 1) is more helpful than the three systems highlighted above. For example, in the marine ovoid species *Magnetococcus massalia* strain MO-1 and *Magnetococcus marinus* strain MC-1, flagella assemble into two clusters on one hemisphere of the cell. The seven

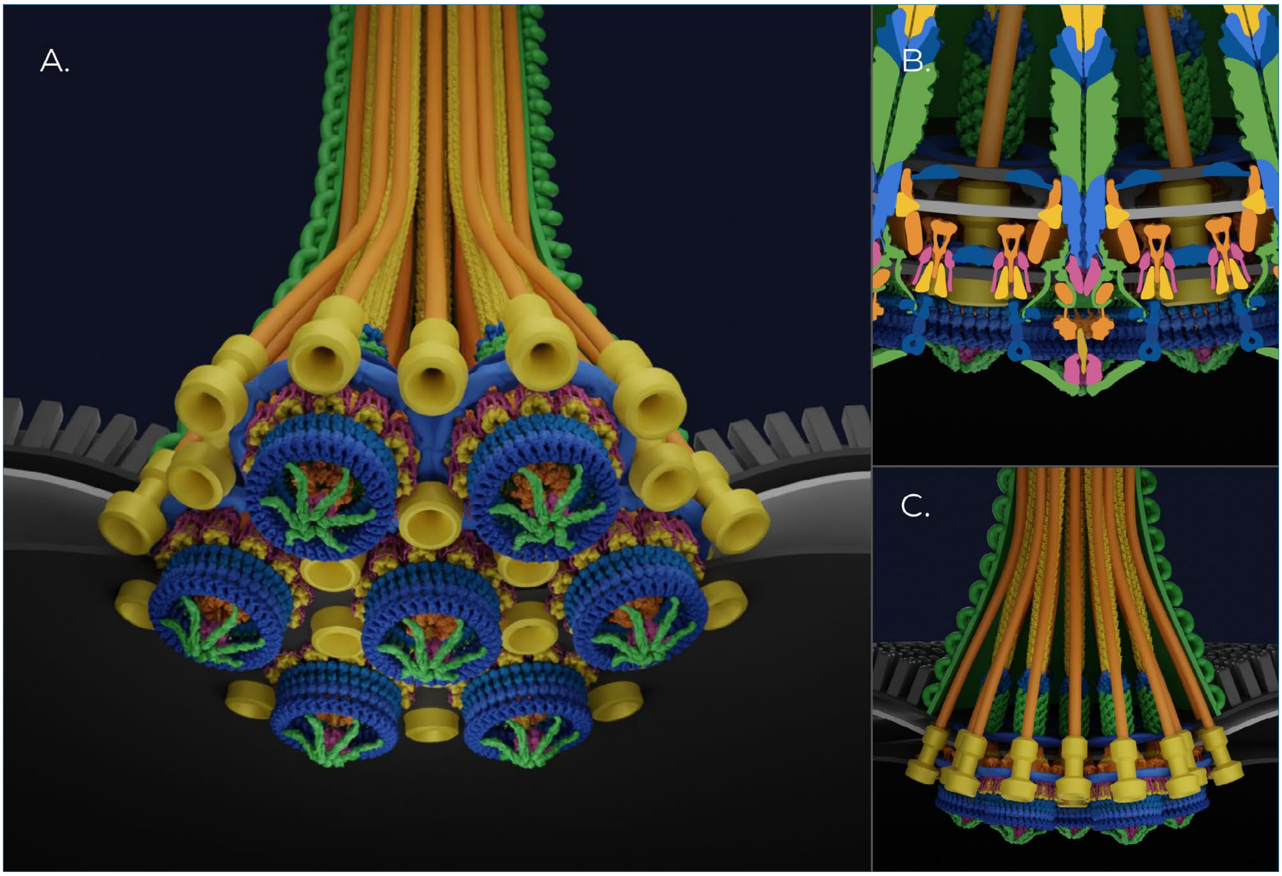

Figure 5. MO-1 hexagonal hepta-motor array (based, in part, on figures 1–6 of ref. 30, and AlphaFold predictions). (A) Low view, (B) cross-section diagram, (C) front view. Note the shorter universal joints compared to other species. MO-1 has two of these arrays located on one hemisphere of their ovoid cell body (see the bilophotrichous arrangement in figure 2).

motors at the base of each cluster form a hexagonally arrayed hepta-motor complex with a 2:3:2 arrangement (figure 5). Several other marine cocci that are magnetotactic have bilophotrichous flagella in a similar motor array architecture.[22,23] A 2017 study found novel magnetotactic cocci that possess an even more complex flagellar motor array with 19 motors arranged in a 3:4:5:4:3 arrangement.[24]

The magnetotactic bacteria represent a diverse group and some can cluster together into spherical or ellipsoidal bundles of 40 to 80 cells.[25] These bundles (called 'multicellular magnetotactic prokaryotes', MMPs) are coated in thousands of flagella, similar to the arrangement of cilia over the surface of single-celled eukaryotic ciliates (figure 4). Through some unknown mechanism, these cells coordinate all their flagella, which is necessary for efficient motility and navigation.[25]

The large ovoid species *Ovobacter propellens* displays a large unsheathed tuft of about 400 flagella, mostly rooted in a depression, and spaced about 100 nm apart at one end of its cell body.[26] This flagellar arrangement does not fit readily into the classification system proposed in table 1.

2. The presence of sheaths surrounding flagellar filaments

The polar flagella of several genera of Gram-negative bacteria are surrounded by a sheath, which is a membranous tube around the filament and is continuous with the cell membrane (figure 1a, d, g, h).[27] (Interestingly, there is one reported case of sheathed peritrichous flagella.[28]) Some membrane proteins and lipopolysaccharides localize to these sheaths, though the exact mechanisms of this localization remain unknown.[27] It is worth noting that when multiple flagella are present on a cell pole, each is surrounded with its own sheath. In contrast, whole bundles of flagella in *Magnetococcus massalia* MO-1 and *Magnetococcus marinus* MC-1 are surrounded with a stretchable sheath made of glycoproteins arranged in a helical array (figure 5).[29,30]

Many functions have been proposed for membranous sheaths, including protecting the filament from the gastric environment, hiding flagellins from the host's immune systems, altering the mechanical properties of flagellar filaments, and improving adhesion to surfaces.[27,31]

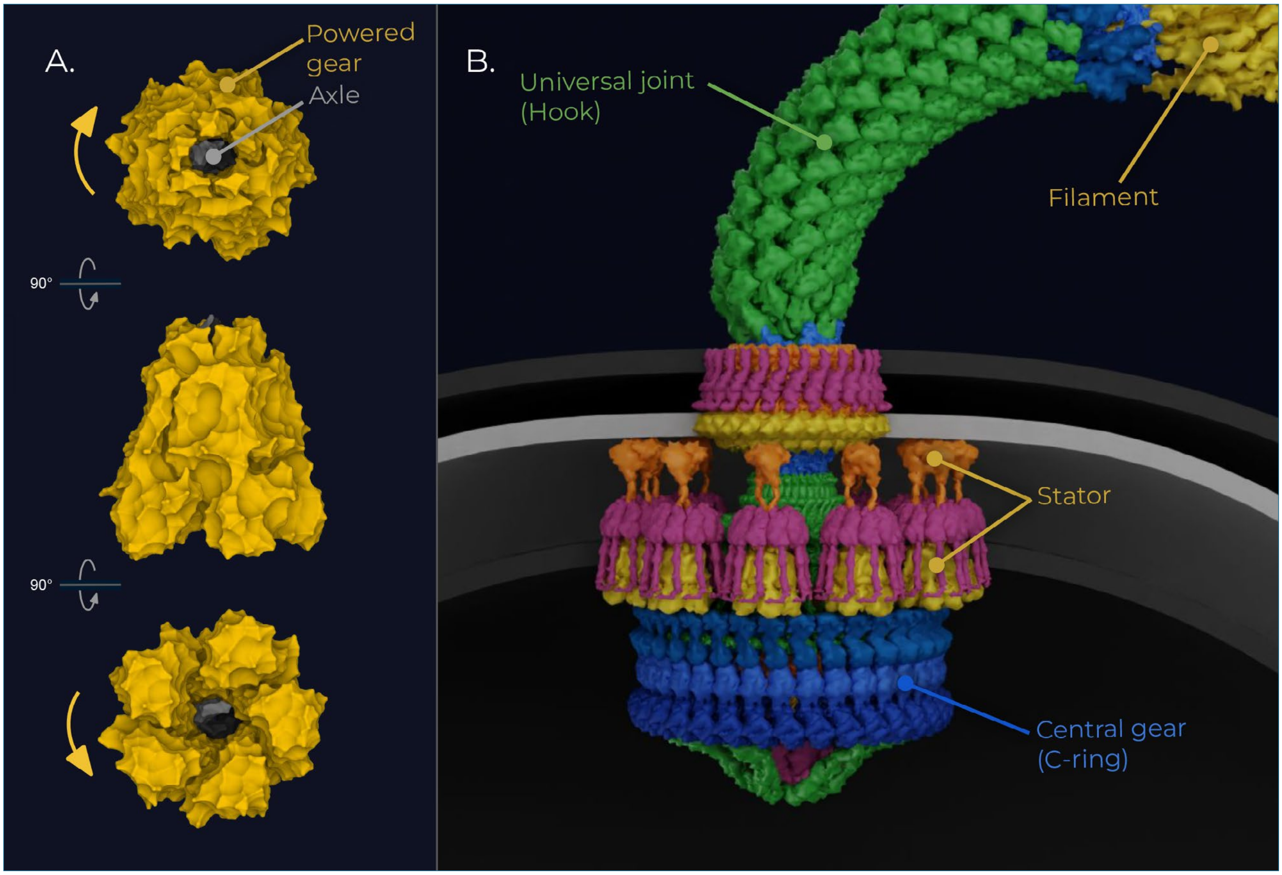

Figure 6. (A) The lower portion of a stator unit (PDB[58] ID: 6YSL, molecular surface representation made in Mol*[62]). The powered gear is shown in yellow and axle is shown in black and grey. The upper portion of the MotB proteins that make the axle are not shown (but are shown in orange in b) (B) The flagellar motor of *E. coli* with the central gear, stators, universal joint and filament labelled.

3. The structure of the parts common to all flagella

With the exception of the L- and P-rings (which are absent in Gram-positive species), the parts discussed in part 1 are found in the flagella of all flagellated bacterial species.[17] This list of parts includes the stators, FliL rings, central gear (C-ring), export apparatus, hub (MS-ring), driveshaft (rod), universal joint (hook), universal joint–filament junction, and propeller filament.[17] It is worth highlighting the spirochete family, as *L. interrogans* has both the L- and P-rings; *B. burgdorferi* has only the P-ring; and *T. pallidum* has neither.[17]

While these parts are present across flagellated species, there is some diversity in their designs. This designed diversity is most clearly seen in the stators, central gear, universal joint, and filament. Below is a brief summary of the diversity of these parts. For more detail, see appendix 1.

Stators

Flagellar stators are units consisting of an axle and a rotating gear which drives the central gear of flagellar motors (see part 1) (figure 6). Stators differ in a number of ways, including the ion their rotation is powered by, the torque they produce, and how they are regulated.[17,32] The most common ion used is H^+ but Na^+ is also used by the stators of some species, especially marine species.[17] For example, H^+-driven MotAB is used by *E. coli* and *S. enterica*, while Na^+-driven PomAB is used by *Vibrio* species.[17]

At least 65 bacterial species use more than one type of stator.[33] For example, *Shewanella oneidensis* MR-1 has a single polar flagellum (figure 1j) driven by both MotAB and PomAB.[34] Likewise, *Bacillus subtilis* uses a mix of MotAB and Na^+-driven MotPS to drive each of its flagella.[35] *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).[34,35]

Central gear

The diameter of the central gear (commonly called the 'C-ring', figure 6b) varies considerably between species.[36] 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

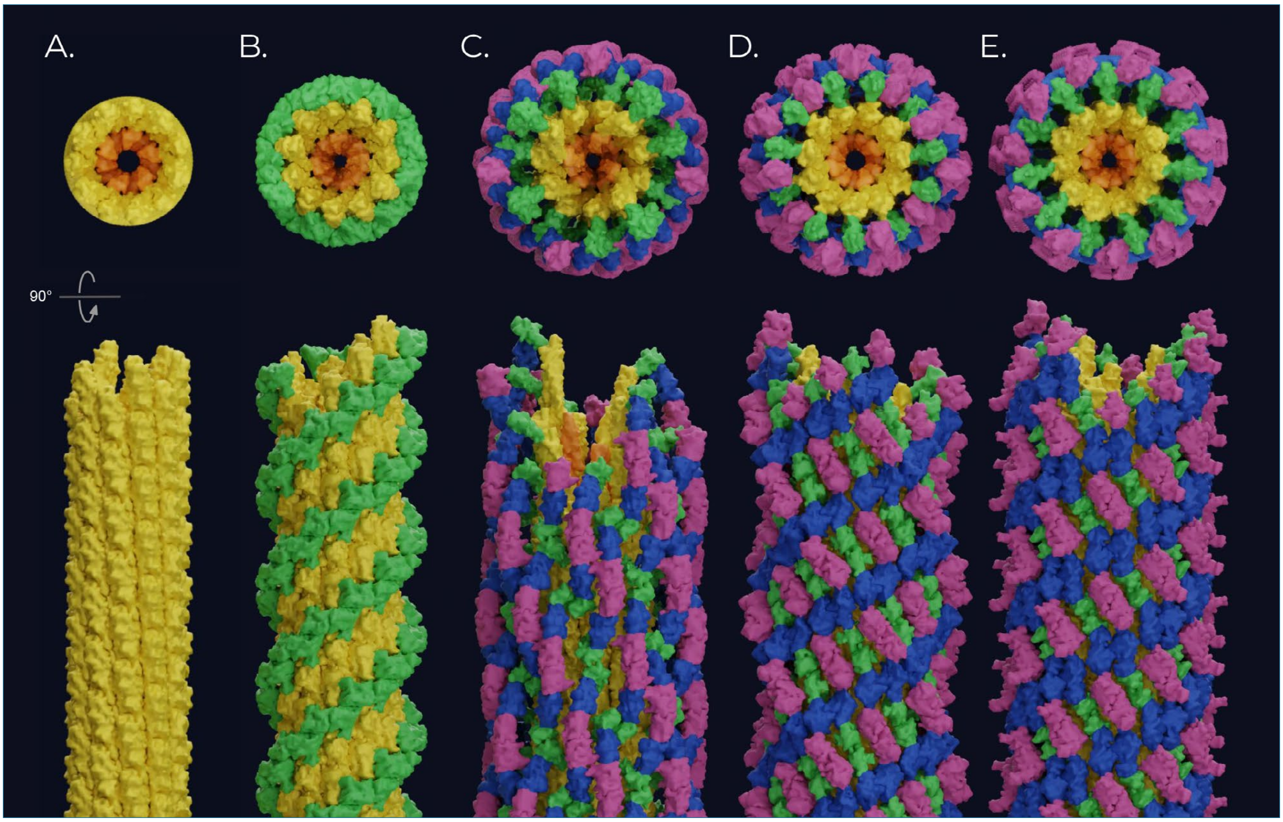

Figure 7. Molecular surface representations of diverse flagellar filament structures coloured by domains (orange = domain 1; yellow = domain 2; green = domain 3; blue = domain 4; pink = domain 5). (A) *C. crescentus* filament (PDB ID: 6XKY) with no outer domains, (B) *Sinorhizobium meliloti* filament 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).

figure 1b with 1c). There is also diversity in the proteins that make up the central gear, including the presence of a protein called FliY, which is used in place of or alongside FliN.[34]

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 differs in its structure, leading to differences in its rigidity, stability, and robustness between species.[37–39]

Filament

The flagellin proteins that make up flagellar filaments differ considerably in the structure of their outer domains.[40,41] Flagellin outer domains can also form dimers or tetramers between subunits to form complex outer-domain sheaths or screw-like structures (figure 7). Glycosylation of flagellins is common in gram-negative species and some gram-positive species.[42] In some species, flagellins are also methylated or phosphorylated.[43,44] Around 45% of bacterial species contain two or more flagellin genes.[45] Typically, in species with multiple flagellin genes, the abundance of specific flagellins is different in the proximal end of the filament from that in the middle and distal end of the filament.[46,47] In spirochetes, proteins bind to the outside of the filament.[48] The filaments of some species (e.g., *E. coli*) switch between a left- and right-handed helix upon a switch in rotational direction. The filaments of other species maintain a constant morphology, either always left-handed (e.g., *V. alginolyticus*) or always right-handed (e.g., *C. crescentus*).[49]

4. The structure of additional parts found in the flagella of only some species

Along with differences in the design of the core parts, the flagella of many species contain many additional parts. This is especially true of high-torque polar and periplasmic flagellar motors which have cage, ring, and/or disk structures around them for structural support (figures 1a–j, m).[50,51] These structures are sometimes referred to as 'stator scaffolds' and can be essential for flagella to function in these species (see part 7).[52] These structures likely serve other functions as well, which future research will uncover. For more detail on these structures in various species see appendix 2.

5. The function of flagella

Flagellum researcher Dr Scott Minnich predicted, from an intelligent design perspective, that flagella would serve more functions than that of just a propulsion device.[53] This is now known to be the case. Flagella are also used for biofilm formation, adhesion, mechanoreception, secretion of virulence factors and/or cleaving peptides.[38,43,54,55] In fact, some non-motile bacteria, such as those of selected species in the genus *Brucella*, use flagella solely for purposes other than motility.[56] However, this lack of motility may be a defect, as other strains of *Brucella* do use flagella for motility.[57]

Conclusion

Bacterial flagella show immense diversity in their design across the bacterial domain, from the number and arrangement of flagella to the presence of additional specialized components like cages and disks. Flagellar designs are optimized for the lifestyles and environmental conditions of a wide array of species. Further research into diverse flagellar designs will surely continue to unveil the brilliance of our Creator.

The next paper in this review series, part 3, will show how flagellar motors change gears and how differences in flagellar arrangement affect the swimming behaviour of bacterial species.

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