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Motility in the epsilon-proteobacteria

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The epsilon-proteobacteria are a widespread group of flagellated bacteria frequently associated with either animal digestive tracts or hydrothermal vents, with well-studied examples in the human pathogens of *Helicobacter* and *Campylobacter* genera. Flagellated motility is important to both pathogens and hydrothermal vent members, and a number of curious differences between the epsilon-proteobacterial and enteric bacterial motility paradigms make them worthy of further study. The epsilon-proteobacteria have evolved to swim at high speed and through viscous media that immobilize enterics, a phenotype that may be accounted for by the molecular architecture of the unusually large epsilon-proteobacterial flagellar motor. This review summarizes what is known about epsilon-proteobacterial motility and focuses on a number of recent discoveries that rationalize the differences with enteric flagellar motility.

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Introduction

Motile epsilon-proteobacteria are found in diverse habitats, most commonly animal digestive tracts or hydrothermal vents (Figure 1). Best studied are the animal digestive tract-associated species [1], prominently the human gastrointestinal pathogens *Campylobacter jejuni* and *Helicobacter pylori*. *C. jejuni* and related species are leading causes of gastroenteritis, yet often harmless commensals of birds [2]. Other members of order *Campylobacterales* are also associated with mammalian intestinal tracts, including *Wolinella succinogenes*, a cattle rumen commensal [3], and pathogenic *Arcobacter* species [4]. *Helicobacter* species are invariably digestive tract-associated, with *H. pylori* colonizing 50% of humans on the planet and although associated with gastritis, gastric ulcers and gastric carcinoma, is also associated with beneficial outcomes with gastroesophageal reflux and asthma, indicating that the relationship between human host and *H. pylori* are more complex than first thought [5–7]. Similar observations of pathogenesis have been made for *H. mustelae* in the ferret gastrointestinal tract and *H. felis* in mice [8], and *Helicobacter hepaticus* causes chronic hepatitis, liver cancer and inflammatory bowel disease also in mice [9,10]. Yet despite numerous examples of digestive tract-associated epsilon-proteobacteria, there are also many environmental species. Many are chemolithotrophs [11] that obtain energy by oxidizing compounds found in their environment. The *Sulfurospirillum*, *Sulfurimonas*, *Sulfuricurvum*, *Thiovulum*, and some *Arcobacter* genera from the *Campylobacterales* order are environmental bacteria [12,13], with habitats ranging from marine hydrothermal vents and coastal sediments [14], underground oil-storage facilities [15], plant roots in salt marsh sediments [16] and pond mud [17]. Intriguingly, there are multiple cases of epsilon-proteobacteria that combine animal association with hydrothermal vent environments by establishing symbioses with gastropods and annelids endemic to vents [18,19].

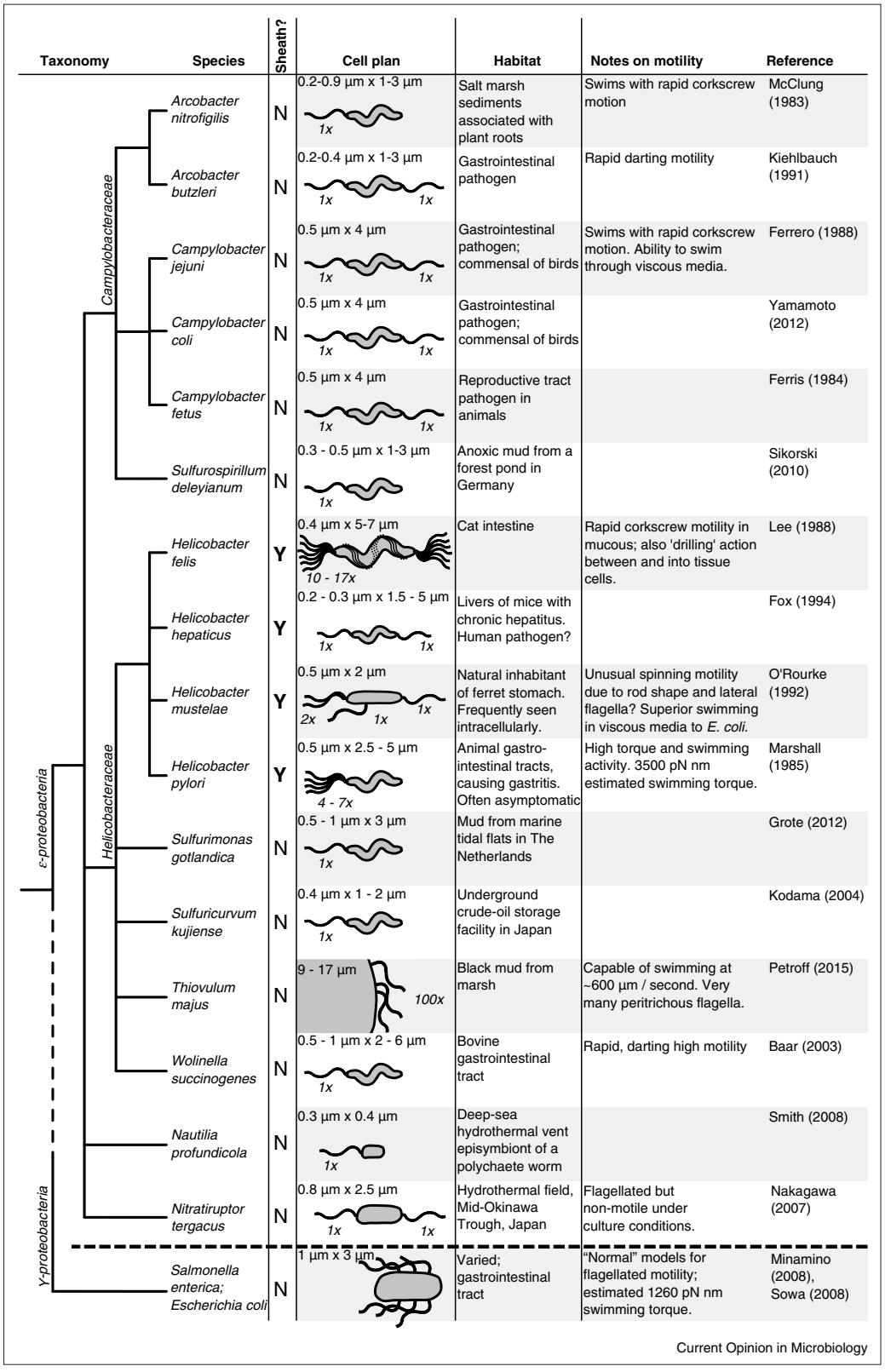
Flagellar motility is important to both pathogenic [2] and hydrothermal vent-associated [20] species. In animal-associated species, motility is crucial for host colonization and virulence by enabling traversal through viscous gastrointestinal mucous [2,21]. Motility is also clearly important for environmental members of the epsilon-proteobacteria as demonstrated by high expression levels of flagellar genes in hydrothermal vent epsilon-proteobacteria [20,22]. In environmental *Thiovulum* spp., flagella play key roles in nutrient acquisition whereby cells attach to surfaces and rotate their flagella to increase oxygen and sulphide flux for metabolism [23••].

Despite using homologous flagellar systems, there are striking differences between epsilon-proteobacterial and the enteric motility models *Escherichia coli* and *Salmonella enterica* sv. Typhimurium. Although enterics are often peritrichous (multiple flagella distributed over the cell body), the epsilon-proteobacteria have one or a few polar flagella. And yet despite generally having fewer flagella, representative epsilon-proteobacteria swim faster than the enterics in low-viscosity media, and continue to swim at high speed even in high-viscosity environments that immobilize the enterics [24–26]. This review highlights the unique features of epsilon-proteobacterial motility that may play a role in their unique range of habitats.

Epsilon-proteobacterial swimming ability

Characteristic of the epsilon-proteobacteria is their ability to swim rapidly, and to continue swimming even in high

Figure 1



An overview of epsilon-proteobacterial cell plan and motility. Notes on motility are described where known. References are listed in *Bibliography*.