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ACOUSTIC STREAMING, THE "SMALL INVENTION" OF CYANOBACTERIA?

FLUJO ACÚSTICO, LA "PEQUEÑA INVENCIÓN" DE LAS CIANOBACTERIAS



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RESUMEN: *Los mecanismos de bombeo en microingeniería aparecieron al principio de la década de los 90. El principio detrás de esto es el de flujo acústico. ¿Ha descubierto la Naturaleza este invento de hace 2.700 millones de años? Algunas cianobacterias marinas de la especie* Synechococcus *nadan 25 diámetros por segundo sin ningún medio visible de propulsión. Especulamos en este artículo que vibraciones de amplitud de nanoescala del estrato S (una cáscara cristalina que cubre las membranas exteriores en las cepas móviles) y con frecuencias del orden de 0,5-1,5 MHz (y esto es factible por los motores moleculares), podrían producir velocidades de deslizamiento del fluido, en el exterior de la frontera de la región Stokes. Dentro de esta capa límite (que para nuestra sorpresa resulta ser relativamente ancha) el comportamiento del flujo es rotacional (y en consecuencia, ventajoso desde el punto de vista biológico). Adicionalmente a este supuesto mecanismo que se podria llamar "nadando cantando", mostramos otros posibles ejemplos biológicos de corrientes acústicas. Sir James Lighthill ha sugerido que el flujo acústico también se da en la cóclea del oído de los mamíferos, y son muy sugerentes los nuevos hallazgos en las células ciliadas externas. Otras posibilidades son flujos acústicos producidos por vibraciones de las membranas en células de levadura, mejorando su química (¡cerveza y pan!), el contoneo de los glóbulos rojos en los tubos capilares y el bombeo de fluido producido por las diatomeas.*

PALABRAS CLAVE: *Flujo acústico; piezolelectricidad; membranas celulares; Synechococcus; cianobacterias.*

ABSTRACT: Micro-engineering pumping devices without mechanical parts appeared "way back" in the early 1990's. The working principle is acoustic streaming. Has Nature "rediscovered" this invention 2.7 Gyr ago? Strands of marine cyanobacteria Synechococcus swim 25 diameters per second without any visible means of propulsion. We show that nanoscale amplitude vibrations on the S-layer (a crystalline shell outside the outer membrane present in motile strands) and frequencies of the order of 0.5-1.5 MHz (achievable by molecular motors), could produce steady streaming slip velocities outside a (Stokes) boundary layer. Inside this boundary layer the flow pattern is rotational (hence biologically advantageous). In addition to this purported "swimming by singing", we also indicate other possible instantiations of acoustic streaming. Sir James Lighthill has proposed that acoustic streaming occurs in the cochlear dynamics, and new findings on the outer hair cell membranes are suggestive. Other possibilities are membrane vibrations of yeast cells, enhancing its chemistry (beer and bread, keep it up, yeast!), squirming motion of red blood cells along capillaries, and fluid pumping by silicated diatoms.

KEY WORDS: Acoustic streaming; piezoelectricity; cell membranes; Synechococcus; cyanobacteria.

1. Overview

This essay is devoted to a little invention by Engineers, that we speculate cyanobacteria anticipated much earlier...

Half way back in the history of life, marine cyanobacteria invented photosynthesis. This spectacular evolutionary innovation shaped the Earth's atmosphere for oxygen consuming life (not satisfied, cyanobacteria invaded land disguised as chloroplasts). Conservative estimates (García *et al.,* 2003) [27] give cyanobacteria 1/2000 of today's Earth's biomass. Current cyanobacteria research ranges from molecular/structural biology and physiology, to Earth science and ecology. Our basic reference is the recent book edited by Antonia Herrero and Enrique Flores, CSIC researchers from Instituto de Bioquímica Vegetal y Fotosíntesis at Sevilla (Herrero and Flores, 2008) [32])[1]. Why study cyanobacteria? If "domesticated", cyanobacteria will afford a new revolution in agriculture and energy[2].

Some Synechococcus strands are able to swim in open sea waters, *without flagella or other known means of propulsion.* Marine biologists were embarrassed that this discovery came only on 1985: "The ocean is full of these things; flagellated bacteria are the oddballs" (Manson *et al.,* 1998) [49]. For a personal account of the surprising discovery of marine cyanobacteria, see (Waterbury, 2004) [95].

Without flagella, something evidently must be happening on the cell's surface. We suggest that Nature experimented 2.7 Gyr ago with a physical effect called *acoustic streaming.* Around 1990 engineers started to use this effect (discovered by Faraday) to produce micro-pumps without mechanical parts[3]. The technology is simple: all they needed were mini-piezoelectric transducers producing "nanoquakes" in the channels.

We hypothesize that the Synechococcus cell membrane has piezoelectric properties that could drive traveling waves just like microengineered pumps. In fact, it is well known that some biological membranes, such as that of cochlea outer hair cells, also have piezoelectric properties (Ashmore, 2008) [2]), only four orders of magnitude higher than any man made material!

We wrote this essay aiming both the general audience and experts. We have set our bibliography to the magic number 100, combining technical and non-technical articles. Technical details of our model are presented in (Ehlers and Koiller, 2010) [20]). Our calculations show that cell membrane vibrations with nano-scale amplitudes and frequencies below 1 MH can produce bulk fluid motion of the order of tens of microns per second. We believe that acoustic streaming explains the motility of Synechococcus, and that many other examples in cell biology should exist. Moreover, as we will discuss, there is a extra bonus: acoustic streaming produces a "chaotic fluid atmosphere" around the cell, that enhances mixing and nutrient uptake.

This Arbor issue is a tribute to Darwin's year-2009, his bicentennial and sesquicentennary of "The origin of species" (Darwin, 1859) [15]. We all admire Darwin for his great scientific work, but his humanitarianism is not so much known. We refer to the wonderful recent book (Desmond and Moore, 2010) [17] about Darwin as the anti-slavery activist and their earlier classic and best-seller (Desmond and Moore, 1991) [18].

Intelligent design believers used to claim that the wonderful flagellar motor is "irreducibly complex", so only by the hands of a Creator it could have been produced. That was a bad call: evolutionary biologists showed conclusively that the flagellar motor simply evolved from "old wheels, springs, and pulleys, only slightly altered", as Darwin used to say 150 years ago. How about the Synechococcus mysterious swimming – is there a hand of the devil? We prefer to attempt a scientific explanation, even at the risk of being wrong. We discuss other current models. Sooner than later, the correct explanation will be found[4]. Hilbert, one of the most influential mathematicians of all times, said in 1930: "Wir müssen wissen. Wir werden wissen."

Dedication. Our scientific minds agree with François Jacob: "Nature is an excellent tinkerer, not a divine artificer". Our hearts feel different. God created women, with their irreducible complexity. To our wives we dedicate this modest essay.

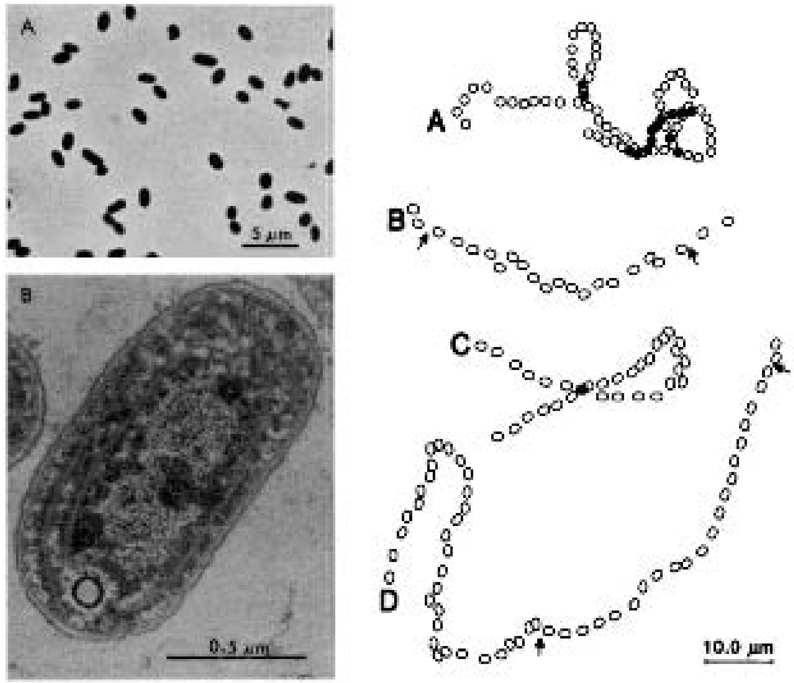

Figura 1. The mysterious open sea swimmer Synechococcus (Waterbury et al., 1985)

2. Piezoelectric materials and acoustic streaming

As parallel reading, we suggest two articles by Juan A. Gallego-Juárez, from the Intituto de Acústica, CSIC/Madrid (Gallego-Juárez, 2007, 2008) [25], [26], for trends and challenges of 21th century acoustics, and particularly *bioacoustics.* For a technical/historical account, see (Beyer, 1998) [10].

2.1. From 1880's to nanophononics/photonics

At the same time that the theoretical foundation for acoustic streaming was being given by Lord Rayleigh[5], the properties of piezoelectric crystals where being discovered by Pierre Curie and his older brother Jacques Curie. That was around 1880.

Piezoelectric materials convert mechanical deformations into voltage differences, and vice versa, so it is a wonderful form of energy transduction. Applications nowadays range from door buzzers, microphones, electric guitars pick-ups, auto-focus on cameras, sensors in cars, to aeronautical and space technology. Piezoeletric-photonic-phononic properties of nano-materials are being intensively studied. As we will discuss in the sequel, *motile Synechococcus have a crystalline outer shell (called "S-layer") with elastic properties.*

Here we do not wish to complicate the model with other possible physical effects, but we cannot refrain mentioning the classical (ie. not quantum) photoacoustic effect. It was also discovered in 1880, by Alexander Graham Bell: light can produce sound. The idea is very simple, transient heat producing pressure differences (this effect is used for optoacoustic imaging in medicine). Cyanobacteria are solar cells. Could thermal expansion-contraction on organelles generate acoustic waves?

Furthermore, one could even speculate that the S-layer has also *photonic-phononic* properties, the quantum version of Graham-Bell's discovery. This subject is totally beyond our scope, so we just refer to two CSIC groups in Spain for this hot topic in nanomaterials. Clivia Sotomayor's group at the UAB/Bellaterra[6] and Francisco Meseguer's group in Valencia[7]. We apologize omitting ~ 300 groups in Spain working in the multidisciplinary nanoworld, in which biology, mathematics, physics, chemistry and engineering are now coming together[8].

2.2. Ultrasound, cavitation, acoustic streaming

For our specific topic, acoustic streaming, we stand on the shoulders of Wesley Nyborg, to whom among other things we all owe the safety of medical ultrasound technology[9]:

> "In a region of fluid where a sound field exists, the pressure and velocity vary with time, but, in general, the temporal averages of these quantities are not zero. The average over time of the velocity is called *acoustic streaming.* It was probably in studies of plates vibrating in air that the first observations of this acoustical phenomenon were made. Faraday (1831) found currents of air to rise at points of maximum vibration amplitude on such plates, and to descend at displacement nodes" (in chapter 7 of Hamilton and Blackstock, 1998, [31]).

Already in 1958 Nyborg suggested that cellular processes could be influenced by ultrasound fields:

> "Certain biological effects may be associated with cellular membrane vibrations set up by external vibrating bubbles... When a cell is immersed in liquid under the action of sound, enhanced local vibratory membrane motion may be expected in the vicinity of any attached compressible body." (Jackson and Nyborg, 1958)

Of course, there are many applications of ultrasound in medicine: imaging, breast cyst evaluation, kidney stone breaking, and more recently, non invasive brain neurosurgery. Most of the studies are devoted to avoid potentially harmful effects of ultrasound. Specially dangerous is the sonic induced collapse of cavitation bubbles. The collapse of bubbles (that can be induced by ultrasound) releases an enormous amount of energy. In fact, this is explored to the utmost extent by the infamous "pistol shrimp", a creature much frightening than sharks. We invite the reader to visit the gallery on the web site of Detlef Lohse, from Twente *http://pof.tnw.utwente.nl/*[10]. Lohse has also videos about Faraday's jets.

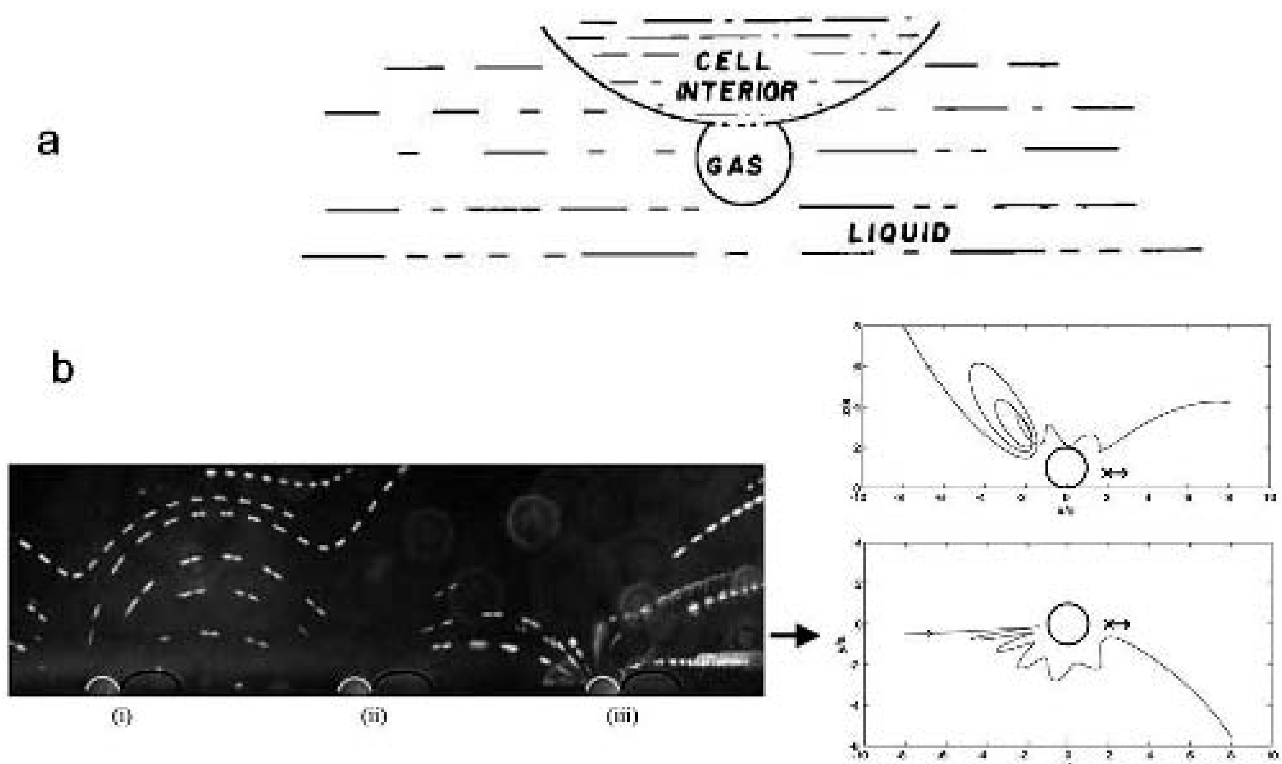

Figura 2. Nyborg predicted that cellular processes could be provoked by acoustic streaming induced by vibrating bubbles. a. Figure sketched in (Nyborg, 1958). b. Philippe Marmottant and collaborators are doing controlled experiments on bubble induced microfluidic transport (Marmottant, 2006).

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As far as we know, there is just one instance where acoustic streaming has been *directly used to model a biological phenomenon.* On the 1991 Conference about Fluiddynamics in Biology, Seattle, Sir James Lighthill, a famous fluid dynamicist and Emeritus Lucasian Professor at Cambridge, proposed a model for the inner year fluid/membrane energy exchange (Lighthill, 1992) [43]):

> "Just as mean motions, usually described as acoustic streaming, can be generated by sound waves, so also those cochlear travelling waves into which incident sound waves are converted in the liquid-filled mammalian inner ear are capable of generating mean motions... Physiological questions of whether this flow may be channelled through the space between the tectorial membrane and inner hair cells, whose stereocilia may therefore be stimulated by a mean deflecting force, are noted here but postponed for detailed consideration in a later paper"[11].

As we explain below, a fundamental requirement for acoustic streaming is *sound attenuation.* Lighthill suggested that, conversely, stereocilia attenuate the sound produced in spontaneous hair cells vibrations, producing streaming flow in the channel bounded by the tectorial membrane (spontaneous otoacoustic emissions?)

It is suggestive to compare images of stereocilia bundles with a famous sculpture of Eusebio Sempere in Madrid.

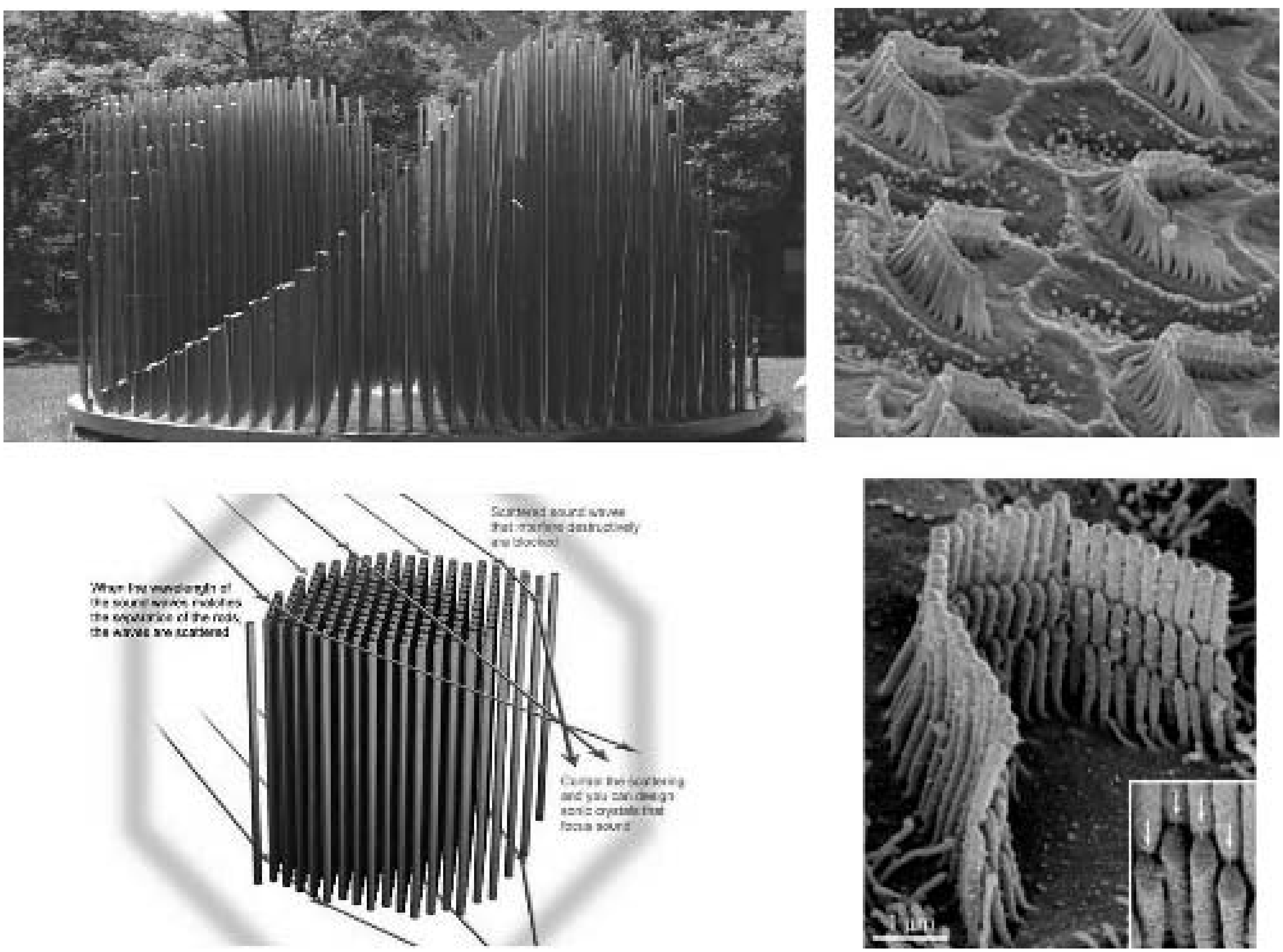

Figura 3. Structures that control sound. Left panel, top: a sculpture by Eusebio Sempere in Madrid. Bottom: from New Scientist comment on Meseguers group study on the attenuation properties of the sculpture (http://www.science.org.au/nova/newscientist/072ns$_0$04.htm). Right panel: hair cells stereocilia, that actively inteact with pressure waves. (Sources: http://www.scripps.edu/newsandviews/e_20030317/mueller2.html////http://www.nih.gov/news/pr/ jun2006/nidcd_27.htm.).

Francisco Meseguer's group has shown that the sculpture does attenuate sound (Martínez-Sala *et al.,* 1995) [51], the vertical bars creating sonic gaps analogous to a nanoscale phononic crystal[12]. Can one feel currents of air around Sempere's sculpture induced acoustic streaming? We anticipate that our model for Synechococcus swimming reverses the above observation by Nyborg, and that another biological counterpart to Sempere's vertical bars will come up. As a motivation, we make a short discussion on the cochlear amplifier.

2.3. Cochlear amplifier: acoustic streaming in the ear itself?

Sound waves collected by the auricle of the outer ear pass through the auditory canal striking the *tympanic membrane* (eardrum). The sound wave is then transmitted through the middle ear through the ossicles consisting of three delicate bones: the hammer that is in contact with the tympanic membrane, the anvil, and the stirrup which is in contact with the oval window of the cochlea[13].

Even the general aspects of the inner ear biophysics are still controversial, and there are several theories. The first model for the mechanics of the cochlea was proposed by Herman von Helmholtz in the 19th century when he suggested that the basilar membrane acts as a frequency analyzer [23]. In the mid-19th century, working with cochleas of cadavers, Georg von Békésy discovered that sound waves induce traveling waves along the basilar membrane that reach a peak amplitude at a characteristic place tuned to the particular frequency [7]. It became apparent however that the sensitivity of the ear could not be fully explained by a passive basilar membrane. In the early 1980's Hallowell Davis coined the term *Cochlear Amplifier* for active processes within the cochlea that amplify and sharpen the sense of hearing [16].

Here we follow Lighthill's idea that localized oscillations of the basilar membrane within the fluid filled cochlea can lead to acoustic streaming sufficient to deflect the stereocilia of the inner hair cells of the cochlea. When the stereocilia are deflected an electric signal encoding the sound wave is sent to the brain. Reptiles do have a rudimentary cochlear amplifier. Mammals do much better. From an engineering point of view the performance specifications of the mammalian ear are incredible. The auditory system of a healthy human is able to detect frequencies ranging from 20 Hz to 20 kHz over a dynamic range of 0 to 120 decibels. The limit of sensitivity is just below the ability to hear heat! The logarithmic decibel scale understates the last point: zero decibels represents the faintest sound the ear can detect and 120 decibels is 1,000,000,000,000 times as intense! Yet the ear is so finely tuned that trained musicians can hear if a piano's A key (tuned to 440 Hz) is off by just 2 Hz. Not to mention bats, that have evolved highly sensitive ears allowing them to navigate and detect insects using a natural form of sonar.

Vibrations of the stirrup on the oval window cause a traveling wave within the fluids of the cochlea. Within the cochlea sounds are decomposed into their component frequencies, converted into an electrical signal and transmitted to the brain. The cochlea is shaped like the shell of a snail with 2 1/2 turns, consists of three fluid filled sections: the scala vestibuli, the scala tympani and the scala media. The scala vestibuli and scala tympani are filled with a fluid called perilymph and are connected at the apex of the cochlea. The scala media is partitioned from the scala vestibuli by the Reissner's membrane and from the scala tympani by the basilar membrane and is filled with a fluid called endolymph with a high concentration of positively charged potassium ions. Sitting atop the basilar membrane is the organ of corti which converts the mechanical sound wave into an electrical signal.

The key to the ability of the ear to decompose frequencies is the structure of the basilar membrane. Each position along its length is tuned to a particular frequency. Near the oval window it is narrow and stiff being tuned to high frequencies. Near the apex of the cochlear duct it is tuned to low frequencies being wide and compliant. The stiffness decreases by four orders of magnitude from the base to the apex. The basilar membrane is constructed of radial fibers allowing a particular place to oscillate nearly independently of nearby places. Mammals have evolved a cochlear amplifier that both increases the amplitude at the characteristic place and sharpens the peak [2]. Amplification, which is between 20 and 30 decibels results from motility of the outer hair cells of the organ of corti in response to a positive feedback control system. The cochlear amplifier allows humans to hear nuances of speech and music over a wide dynamic range of intensity. It is safe to say that human onlookers are more charmed by a snake charmer's flute than is the snake!

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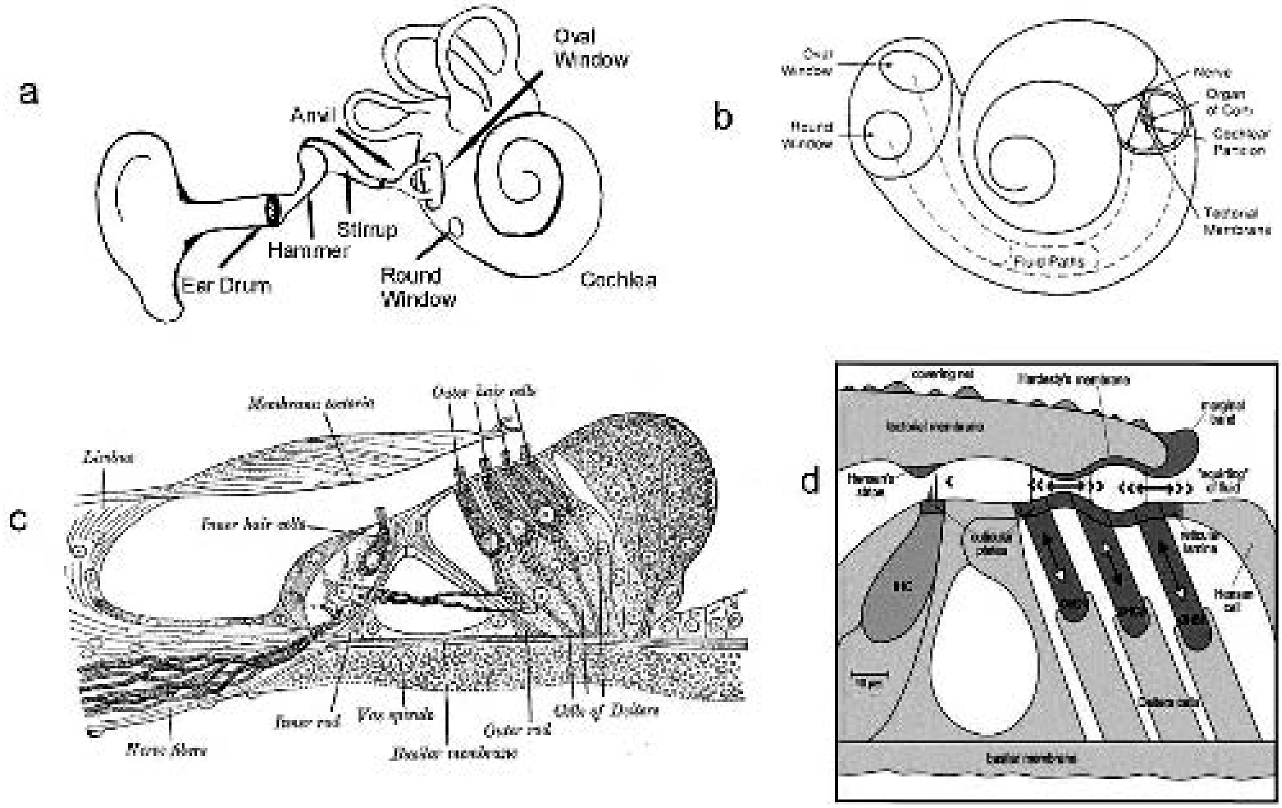

Figura 4. a. Outer and inner ear structures. b. Sketch of cochlea morphology c. Cochlea cross section (Greys anatomy) d. Dynamic interaction between outer and inner hair cells (Bell and Fletcher, 2004).

While the hairs of the outer hair cells are deflected by direct contact with the tectorial membrane inner hair cells are deflected by motions of the endolymph itself. This is where acoustic streaming could play a role. Lighthill shows that significant acoustic streaming occurs near the characteristic place. He could not complete his theory outlined in (Lighthill, 1992) [43]). The cochlear amplifier mechanism is a theme of intense debate among the experts (see *http://www.mechanicsofhearing.org/* for their regular meetings), but nonetheless we took the nerve to make a small speculation in [20], about a fluid mediated amplification, involving a positive feedback between the inner and outer hair cells.

2.4. Physics and mathematics of acoustic streaming

Acoustic streaming is a subtle phenomenon. Water is usually assumed to be an incompressible fluid in microswimming modeling, but acoustic streaming takes into account that it does have some degree of compressibility. AS is a nonlinear, second order effect, and even for highly viscous flows part of the inertial term in the Navier-Stokes equation must be retained.

The Navier-Stokes equation is the fundamental equation in fluid mechanics. It depends in one parameter, the Reynold's number, that essentially gives the ratio between inertial with respect to viscous forces. It ranges from about zero in microswimming (10^{-4} for spermatozoa) locomotion to the order of one million for birds and fishes (10^{8} for a blue whale)[14].

It is the *attenuation* of sound, due to viscosity, that creates a gradient in the momentum flux, resulting on a steaming flow. In air, turbulent jets (quartz winds) with speeds of up to 10 cm/sec can be generated in front of the face of a quartz crystal excited with an electrical current. For the mathematically inclined reader we suggest the review (Riley, 2001) [77]), with a broader view of AS called *steady streaming.*

Mathematically, *rectification* almost invariably involves a time averaging process, second order in the amplitude of the vibrations. To indicate why this is so, we finish this section with an "abstract nonsense", with the aim at calling attention to *Geometric Mechanics*, a subject of our special interest[15].

Many control processes can be viewed in terms of mappings from a space of controls[16] S to a space of states Q. Q has locally the form of a product $Q \sim G \times S$, where the controls are viewed as "shapes" and the elements of G represent "locations". For locomotion, the problem consists of finding a time-periodic choice $s(t)$ in S, so that after one period the state returns to the same "shape" but has moved in the desired direction (if possible in an optimal way). This net motion, that mathematicians call *holonomy*, is proportional to an "area" of a 2-dimensional disk bounded by the closed curve $s(t)$.

Having been developed in the last 30 years by mathematicians of a high scientific level such as Vladimir Arnold, Alan Weinstein and Jerry Marsden, Geometric mechanics connects with all areas of pure mathematics. In addition, Roger Brockett has leaded the foundations of Geometric Control. In fact, the geometric mechanics approach has been useful in applications ranging from industrial robotics to molecular reactions. Spain and Latin America are doing well in this area, having their hub at the Instituto de Ciencias Matemáticas/CSIC at Madrid[17].

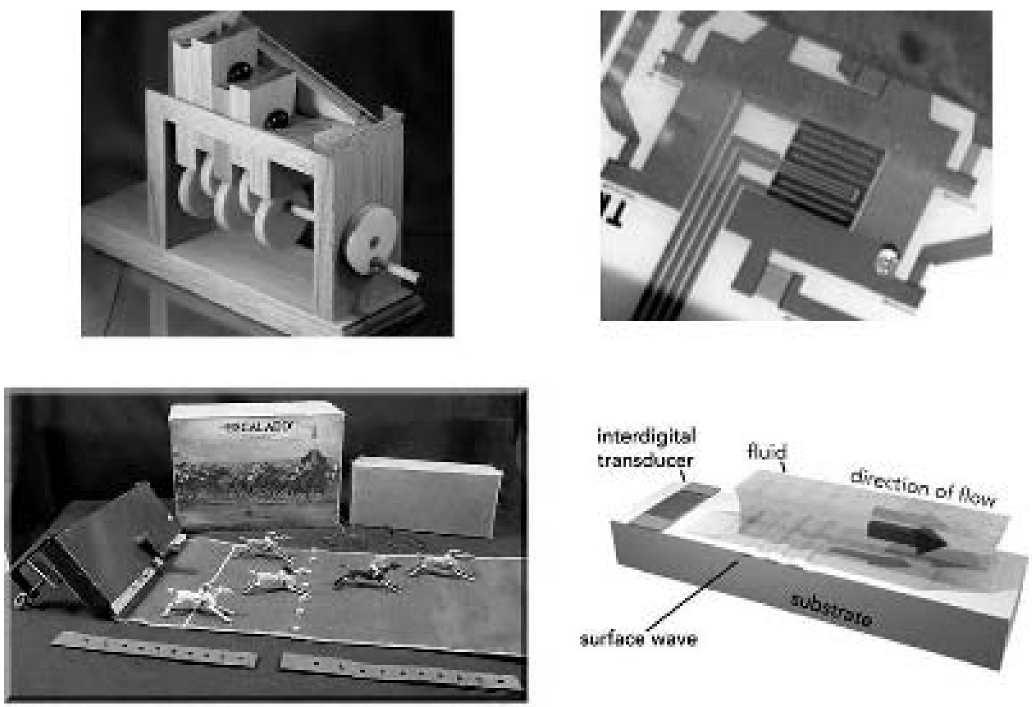

Figura 5. Left panel. Geometric mechanics: Toys that rectify small scale vibratory motion, producing bulk motion. Right panel. Acoustic streaming is a rectification phenomenon (from Advalitix web site).

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3. A FLASHBACK TO 25 YEARS AGO AND RECENT FINDINGS

3.1. Microchips that pump water without mechanical parts

Around 1990 Richard Moroney, then an Electrical Engineering graduate student at Berkeley, began to experiment with acoustic streaming on channels cut on microchips. One of us (KE) eye-witnessed the original setup. At that time, for his dissertation at U.C. Santa Cruz, he was modeling the snakelike microswimming of Turbatrix aceti (a nematode commonly found in unfiltered vinegar) and came often to Berkeley. Together with his advisor Richard Montgomery, they visited White's lab to meet with Moroney. Fifteen years after that visit the idea came, as a strike, that acoustic streaming could also be a driving mechanism in cell biology.

Moroney described the first MEMS acoustic streaming device as follows (Moroney, White and Howe, 1990, [59])[18]:

> "We have observed fluid motion induced by traveling flexural waves in 4 μm thick membranes using 2.5 pm diameter polystyrene spheres in water to make the fluid motion visible... their velocity is in the direction of wave propagation and is proportional to the square of the acoustic amplitude. The maximum speed is 130 pm/s for an RF drive voltage of 7.1 Vrms at 3.5 MHz; the wavelength is 100 μm. Sphere motion has been observed in regions without acoustic waves, suggesting fluid recirculation. Standing Lamb waves, which can be seen visually with a phasecontrast microscope, are found to trap particles, including bacteria located in a drop of water that contacts the membrane... Possible applications include temperature redistribution in ICs (integrated circuits) and miniature chemical processing systems".

An account of the perspectives on the field by the end of the 1990's is given by (White, 1997) [96]. "What good is a new-born baby?", said Faraday to impatient Gladstone. Governments are collecting taxes on acoustic streaming. A thriving company is Advalytix (*http://www.advalytix.com/*), founded in 2000 as an spin-off of a consortium of German universities[19]. One of the co-founders is Axim Wixforth, from the Physics Department at Augsburg[20]. For work being done in other labs, see the program of the recent meeting *http://*2009*prato.net/Home.html.* We suggest seeing the interesting videos in the site of the Micro/NanoPhysics Research Laboratory, Monash University, Australia[21].

3.2. Cells that swim without flagella

As we mentioned in the overview, in October 1985, a group of young marine biologists at Woods Hole, lead by John Waterbury[22], reported a strange find, the first observation of a *motile* cyanobacterium.

> "A novel cyanobacterium capable of swimming motility was isolated in pure culture from several locations in the Atlantic Ocean. It is a small unicellular form, assignable to the genus Synechococcus, that is capable of swimming through liquids at speeds of 25 micrometers per second. Light microscopy revealed that the motile cells display many features characteristic of bacterial flagellar motility. However, electron microscopy failed to reveal flagella and shearing did not arrest motility, indicating that the cyanobacterium may be propelled by a novel mechanism." (Waterbury, 1985) [94]

The official world record is 40 μm/sec (in scale, twice as fast as Usain Bolt). As they swim, cells rotate about the translation direction, like a corkscrew, i.e, in a "drilling" fashion). If, by chance, attach to a microscope slide, cells will spin about the point of attachment with equal chance of going clockwise or counter-clockwise (flagellated cells also spin if attached to surfaces). Synechococcus swims in irregular loopy paths, but are known to be are chemotactic to nitrogen compounds. How they direct their average movement has yet to be explained.

3.3. Recent studies on cyanobacterial external membranes

Twenty five years later, Synechococcus swimming remains a mystery, but perhaps time is ripe for unraveling the motility mechanism. During her Ph.D. thesis work at Scripps, San Diego, Jay McCarren (now at MIT) and her advisor Bianca Brahamsha identified two molecules, SwmA, SwmB, required for swimming capability and crystalline S-layer formation. Follows a paragraph from the introduction[23]:

> ... Ehlers *et al.* point out that longitudinal compression waves would be sufficient to propel microorganisms and

> that such waves would not generate any cell shape change. Further calculations estimate that a combination of transverse and longitudinal waves 20 nm in amplitude, 200 nm wide traveling at 160 μm/sec could produce the swimming speeds observed in marine Synechococcus. Such waves are small enough to be consistent with the lack of detectable shape change of cells during swimming. Paying particular attention to the cell surface, as it appears to be of special importance for non-flagellar swimming, one cell surface component has been identified that is required for swimming motility. SwmA is a glycosylated 130 kDa protein that is associated with the outer membrane of the cell... SwmA is clearly required for motility and may be involved in the conversion of torque into thrust. How these cells produce torque and the role of SwmA in the generation of thrust remains a mystery. There are undoubtedly more components of the motility apparatus that have yet to be discovered. (McCarren, 2005) [57]

Indeed, soon afterwards they found another glycoprotein involved in motility, SwmB. The full genome of strand WH8102 was sequenced in 2003 by a team leaded by Brian Palenik, Scripps research director (Palenik *et al.,* 2003, [63])[24]. A rival team simultaneously sequenced another marine cyanobacterium, Prochlorococcus, discovered only in 1988, that shares with Synechococcus the fundamental role in the marine ecosystem[25]. The hype on the achievement can be appreciated from a news release:

> "It's amazing", said Palenik, "that marine Synechococcus were only discovered in 1978. So in 25 years we've gone from not knowing they were there to suddenly knowing every base pair of DNA". With the genomes in hand, researchers will have a better idea of how to solve mysteries surrounding these organisms, such as how they thrive in the nutrient-poor open ocean. Palenik believes such marine genomic information will help in the long run in understanding biodiversity and its conservation. "We've always been trying to understand how diverse our planet's organisms are... These results are helping us do that. Starting to decipher whole genomes of different groups of organisms will help us understand how diverse they are and why they are diverse. These organisms are known for their unique type of swimming, and this newly uncovered fact will shed light on how these organisms can convert chemical energy into swimming motion. (*http://scrippsnews.ucsd.edu/Releases/?releaseID* = 586)".

Many bacteria have S-layers, crystalline "coatings" over the outer membrane. In cyanobacteria they occur in 16 genera, but interestingly, on a given genera not all strains have them. For biological information, see the reviews (Hoiczyk and Hansel, 2000) [24] and (Smarda *et al.,* 2002) [84]. See (Schuster, Pum, Sleytr, 2008) [82] for a review of the use S-layers in bionanomaterials, and (Smit, 2008) [85] for the potential in biotechnology.

How about the physical properties of S-layers? Elasticity properties are being studied by the group of José Luis Toca-Herrero, from CICbiomaGUNE (Centre for Cooperative Research in Biomaterials, *http://www.cicbiomagune.es/*) in San Sebastian, in collaboration with the Nanobiotechnology group at Universitat fur Bodenkultur. See (Martín-Molina *et al.,* 2006) [52] for measurements on their elasticity properties. As far as we know, at the moment there are no reports on other physical properties of S-layers.

The membrane structure of cyanobacteria has a unique complexity among bacteria, since photosynthesis and respiration are performed in the adjacent thylakoid membranes. The study of dynamical processes ocurring in the membrane is in its infancy. We refer to chapter 10 of (Herrero and Flores, 2008) [32], written by Himadri Pakrasi and Michele Liberton fromWashington University at St. Louis. Pakrasi's group participates in the "membrane biology grand challenge", a project sponsored by the Environmental Molecular Sciences Lab/US Dept. of Energy (*http://www.emsl.pnl.gov/root/science/membrane/*). Their model organism is Cyanothece, a cyanobacterium that has a double life, meaning that the circadian rhythm oscillated between photosynthesis and nitrogen fixation.

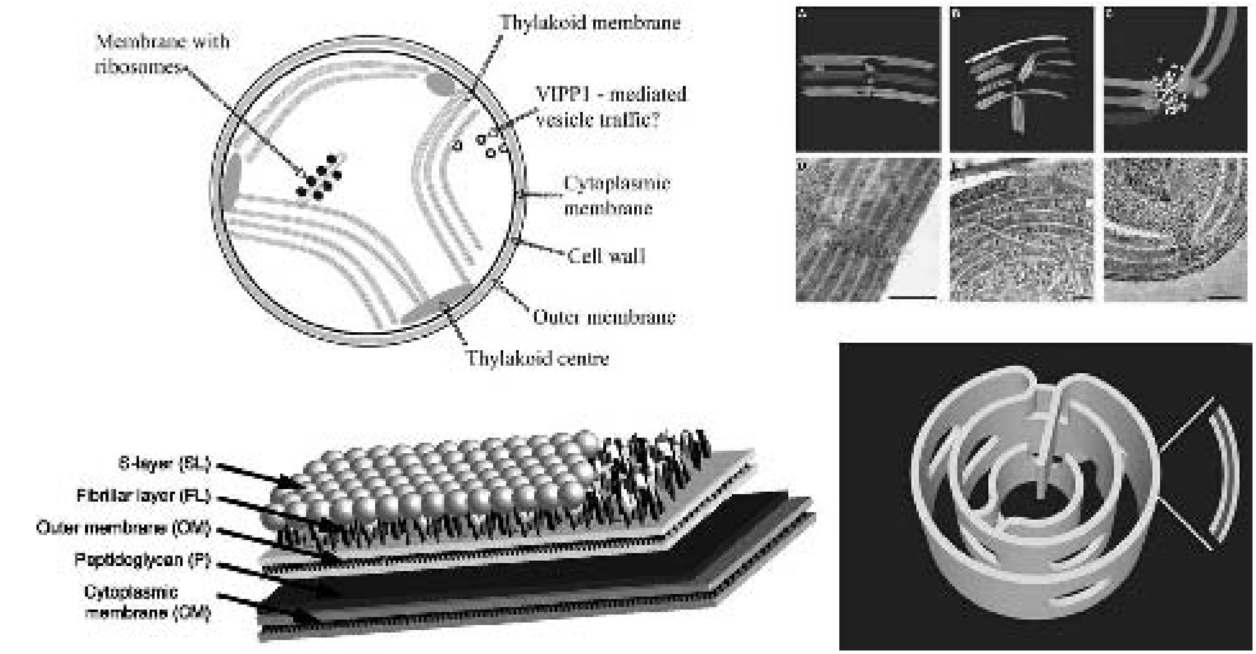

Figura 6. Left panel: cyanobacteria main structures (Herrero and Flores, 2008). Right panel: thylakoid membranes look like multi-connected Riemann surfaces (Nevo et al., 2007).

3.4. Recent studies on thylakoid membranes and photosynthetic systems

Cyanobacteria possess two other notable structures, carboxysomes and thylakoid membranes. Carboxysomes, discovered only in the 1960's, are polyhedral protein shells of around 100 nm diameter, whose surface is made mostly by hexagons (and some pentagons, like a soccer ball) They are the storage bins for CO2. Since they do not seem directly connected to motility (but one can never be sure in biology) we will not discuss them here. For a recent reference see (Tanaka *et al.,* 2008) [87][26]. It seems that they are folded from planar sheets, like an origami!

Thylakoid membranes are the cell battery chargers, that is, they contain the photosynthetic machinery. As we read about their morphology, and about the thylakoid centers where they meet adjacent to the membranes, we could not stop conjecturing that the may have a direct power generating role for Synechococcus swimming.

It turns out that the cyanobacteria developed two distinct photosystems, PSI and PSII, that function in series inside the thylakoid membranes. As described in (Herrero and Flores, 2008, chapter 9) [32], cyanobacteria had to develop a sophisticated regulatory system so that the two photosystems do not "short circuit and burn out". However, if a recent discovery by Arthur Grossman's group at Stanford (Bailey *et al.,* 2008) [5] is confirmed, open sea cyanobacteria break the normal safety regulations! Worse, marine cyanobacteria, that have the good reputation of being responsible for an estimated 20 to 40% of chlorophyll biomass and carbon fixation in the oceans (Palenik *et al.,* 2003) [63] may not be such good guys. We take from a press release *http://www.ciw.edu/news/new_twist_life_s_power_source:*

> "It seems that Synechococcus in the oligotrophic oceans has solved the iron problem, at least in part, by short-circuiting the standard photosynthetic process", says Grossman. "Much of the time this organism bypasses stages in photosynthesis that require the most iron. As it turns out, these are also the stages in which carbon dioxide is taken from the atmosphere."
> In the newly discovered process, a large proportion of these electrons are not used to fix carbon dioxide, but instead go to putting the water molecules back together, which results in much less net oxygen production.

> "It might seem like the cells are just doing a futile light-driven water-to-water cycle," says Bailey. "But this is not really true since this novel cycle is also a way of using sunlight to produce energy, while protecting the photosynthetic apparatus from damage that can be caused by the absorption of light."...
> "This discovery represents a paradigm shift in our view of photosynthesis by organisms in the vast, nutrient-starved areas of the open ocean", says Joe Berry of the Carnegie Institution's Department of Global Ecology. We now know that some organisms short-circuit this complicated process, using light in a minimalist way to power cellular processes directly with a far simpler and cheaper (in terms of scarce nutrients such as iron) photosynthetic apparatus."

Finally, we turn now into recent findings about the morphology of the thylakoid membranes. In the two dimensional pictures of sections of cyanobacteria, these membranes look like concentric cylinders or a series of crescent moons. Very recently, the group of Ziv Reich at Weizmann Institute established that these structures are all interconnected (Nevo *et al.,* 2007) [60]. The surface topologically like a flattened donut with many holes. The analogous surface in mathematics is called a "Riemann surface of high genus".

> "In most cyanobacteria, the photosynthetic membranes are arranged in multiple, seemingly disconnected, concentric shells. In such an arrangement, it is unclear how intracellular trafficking proceeds and how different layers of the photosynthetic membranes communicate with each other to maintain photosynthetic homeostasis. Using electron microscope tomography, we show that the photosynthetic membranes of two distantly related cyanobacterial species contain multiple perforations. These perforations, which are filled with particles of different sizes including ribosomes, glycogen granules and lipid bodies, allow for traffic throughout the cell. In addition, different layers of the photosynthetic membranes are joined together by internal bridges formed by branching and fusion of the membranes... Notably, we observed intracellular membrane-bounded vesicles, which were frequently fused to the photosynthetic membranes and may play a role in transport to these membranes."

We wonder, what if the excess energy from that "dangerous" short circuiting could be diverted productively for locomotion? Can the interesting morphology of the thylakoid membranes be used to some mechanical purpose?

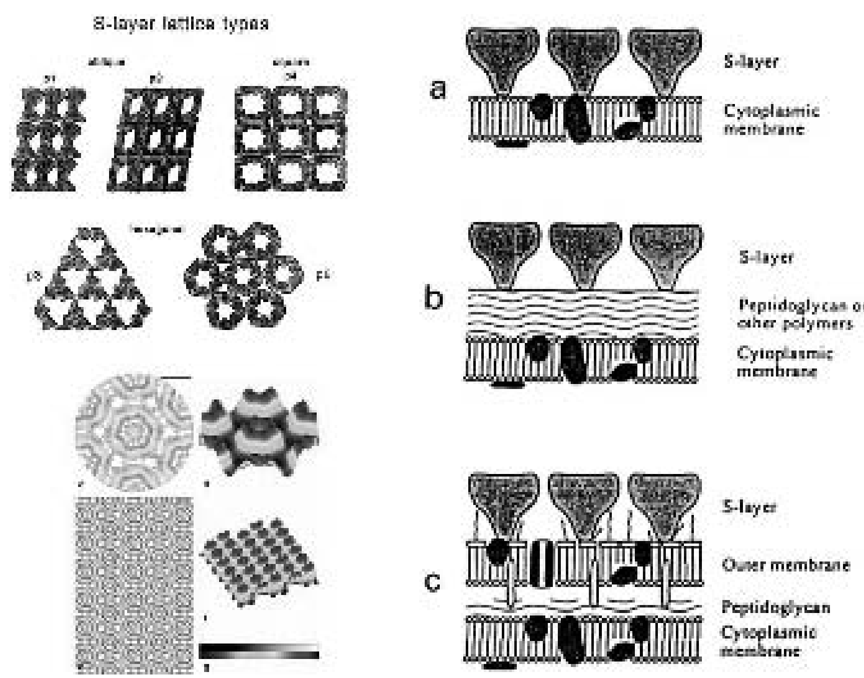

Figura 7. S-layer structures (Smarda, 2002). The crystalline shell has elastic properties, and is a promising biotechnology tool. Its photonic/phononic properties should be investigated as well.

4. The current models

The Synechococcus swimming mystery was introduced to us by Howard Berg, in a mini course he gave in Rio de Janeiro in the early 1990's. Berg is a leading biophysicist from Harvard, who discovered in the 1970's that flagella of bacteria are powered by a rotary motor. Videos on Synechococcus can be seen in his site[27]. First we describe the "standard model" for Synechococcus swimming (Ehlers *et al.,* 1995) [21]: compression-expansion waves. One of us (K.E.) had this idea during his postdoctoral work while swimming in the beaches of Rio[28].

Then we discuss a hypothesis put forward by Aravi Samuel, a former student of Berg, in the early 2000's [78]. In this work the authors report that a motile strand of Synechococcus has a forest of "spicules" projecting outside the S-layer. The authors speculated that these mini rigid flagella could perform rowing motions (as in a "galley slave" cartoon). However, on purely hydrodynamical grounds, this mechanism seems to be very inefficient (or totally, due to the reversibility of the Stokes flows). It has been suggested, moreover, that the spicules could be an artifact of the experiment. Be as it may, our original idea for the acoustic streaming model came from the possibility that the spicules could act as "pressure drummers" on the S-shell.

Very recently, another possible source of surface waves (either mechanical or acoustic) was identified on myxobacteria, involved in their gliding motility: rotating helical structures inside the cell. For completeness, we summarize the findings and provide recent references. A theoretical model is about to be submitted by George Oster's group[29]. Oster (personal communication to K.E.) believes that a similar structure will be found in Synechococcus.

4.1. The "standard model": compression-expansion waves

Briefly, the idea goes as follows. Hold the cell still (say, using an optical tweezer). Suppose the external membrane is a smooth surface that can perform tangential and/or normal deformations. (the standard model does not address the fundamental question on how these compression-expansion waves are produced). If the deformations are only tangential, the *unparametrized shape* of the cell does not vary and one sees nothing by optical microscopy. However, because of viscosity, the liquid does not slip at the contact points. Mathematicians like to impose this type of boundary conditions in "elliptic partial differential equations". Our PDE (called Stokes or creeping flow equations) is of elliptic type because, as we discuss below, the inertial effects are neglected.

The Stokes equations for the external flow can be solved with any given *field of velocities* at the boundary (the instantaneous membrane deformations). From the solution we can compute the *field of forces* along the boundary at any instant of time. Integrating along the surface we get the *net force and torque* that the cell is exerting on the fluid.

The first "geometric" argument (there is a second one): if the optical tweezer is turned off, the cell is free to move. It will therefore translate and rotate rigidly for an infinitesimal time so that the corresponding Stokes drag and torque counterbalances that net force and torque previously computed when the cell was held. The reason why the total force and torque exerted by the cell on the fluid is zero at each instant is that *inertia plays no role in the physics of swimming at the microscopic scale.* It is explained in delightful way in the article *Life at low Reynolds numbers* (Purcell, 1977) [69]. For deforming surfaces – more simply, for a robotic swimmer consisting of a three linked segments – any reciprocal sequence of motions will lead to the "oyster paradox": in the end of the cycle the cell returns to the same place.

Now comes the second geometric argument. If the cell produces a periodic, non reversible, progressing wave along the surface, this can be regarded as a closed curve on an abstract "shape space". The net motion is of second order relative to the wave amplitude, or to the *area* swept in this shape space. Abstractly, the organism does a "gauge theory on a principal bundle". This analysis works well no matter if we have an actual deforming membrane or a virtual geometric surface, enveloping the tips of a ciliated microorganism. More details can be found in the article for La Gaceta de la RSME (Koiller, 1999) [38].

4.2. Rowing with spicules

On Howard Berg's web site one can find the following description of a recent study by one of his ex-students, Aravi Samuel (one of Kurt's collaborators in the standard model).

> "Aravi Samuel tried freeze-slamming a cell sample at liquid-helium temperature at Woods Hole, in the laboratory of Tom Reese. A whole new world opened up: the cell is completely covered by fine hairs a few nm in diameter by about 0.15 μm long! The roots of the hairs go through the outer layers of the cell wall all the way to the inner membrane, where energy for motility is available from an electrochemical gradient."

These hairs, called "spicules", were proposed to function as oars:

> "If motors concealed in the cell membrane or outer membrane are capable of contracting and expanding in a regular manner (perhaps in analogy to the motor protein embedded in the basolateral membrane of cochlear outer hair cells that contract and expand to set the length of the cells), these oscillations would be transduced into a rowing motion of the spicules. In this case, the crystalline surface layer could serve as oarlocks for the spicules, converting smaller motions at the bases of spicules into larger motions at the tips (Samuel, Petersen, Reese 2001) [78]".

The "galley-slave" idea was analysed mathematically by George Oster's group (Wolgemuth, Igoshin, Oster, 2003) [98]. Their estimates for overall motion are compatible with the standard model. However, the very existence of the spicules forest in strand 8113 has not been conclusively confirmed. Jay MacCarren did not find spicules in strand 8102 (MacCarren, 2005, chapter 1) [57], where she reports a personal conversation with Tom Reese that the spicules could be an artifact of preparation.

Nonetheless, we appreciated the analogy with the outer hair cells basolateral membranes in the above quote from Samuel's paper. In fact, if the spicules existence is confirmed we would say "enhorabuena"!

4.3. Swimming by singing

In our theory we have another role for spicules, that of attenuating sound as in Sempere's sculpture's rods. At this point it is important to recall the memorable quote by Lighthill, from a general lecture given at the Institute of Acoustics at Cambridge (Lighthill, 1978) [42]:

> "Not only can a jet generate sound, but also sound can generate a jet!".

How about if, turning around Nyborg's observation, cell membrane vibrations produce external fluid streaming? These vibrations could be powered by intracellular molecular motors[30] located adjacently to the cell membrane, coated with the S-layer, a material with elastic/piezoelectric properties[31]. Cyanobacteria have gas vacuoles and/or other contratile organelles attached to the cell's outer sheath (Walsby, 1994) [93]. These vesicles do resonate with low intensity ultrasound. In addition, the spicules help to enhance streaming by their attenuating/directioning role.

In short: the purported crystalline shell/vacuole/spicules engine could generate external surface acoustic waves (SAWs). If the cell is held (say by an optical tweezer) if would pump fluid adjacent to the membrane. Released, it swims!

Furthermore, acoustic streaming predicts the existence of a turbulent-like boundary layer around the cell, called *Stokes layer,* in which the SAW wave is being attenuated (we estimate the width to be 150 nm). A high frequency traveling SAW is generated on the crystalline outer layer of the cell leading to boundary induced streaming. The progressive wave induces a steady slip-velocity at the outer edge of the Stokes boundary layer. We found that the Lighthill efficiency for boundary induced streaming, which approaches 1%, compares favorably with flagellar propulsion. The amplitude of the SAW necessary to drive an organism the size of Synechococcus at observed speeds is on the order of 10^{-7} cm, too small to be resolved using light microscopy. Synechococcus can propel itself at 25 diameters per second using an $\omega = 1.5$ kHz traveling SAW with wavelength $\lambda = 10^{-5}$ cm and amplitude 9.5×10^{-7} cm. The efficiency is $\eta = 0.39$, about 2.5 times that for the standard model, all other things being equal. Note that the predicted Stokes layer is rather thick.

The acoustic streaming model builds upon the standard model. From the mathematical perspective, the geometric surface on the latter does not actually need to be a material surface. The previous velocity fields in the surface are now viewed as *slip velocities in the boundary of a chaotic (mixing) Stokes boundary layer surrounding the cell.*

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But there is an obvious biological advantage from the existence of this Stokes boundary layer in which the motion is rotational and essentially mixing, inherent to the AS model: *enhanced nutrient uptake and metabolic rates.*

Frequency (Hz)	Amplitude (cm)	Power (Watts)	η (%)	Stokes layer (cm)
500	1.64×10^{-6}	1×10^{-15}	1.17	1.78×10^{-3}
1000	1.16×10^{-6}	2×10^{-15}	0.59	1.26×10^{-3}
1500	9.49×10^{-7}	3×10^{-15}	0.39	1.00×10^{-3}
5000	5.20×10^{-7}	1×10^{-14}	0.12	3.99×10^{-3}

There is a "philosophical" advantage as well: Synechococcus must know that "$f = ma$". This goes against the dominant view, that microorganisms pass their exams just with Aristotelian physics (forces proportional to velocities). In principle, the Stokes paradox can be circumvented by acoustic streaming: a standing reversible wave can propel a cell body. This is because in the AS equations, some portion of the inertial term of the Navier-Stokes equations is retained, even in the low Reynolds regime. For details, see (Ehlers and Koiller, 2010) [20]).

4.4. "Egg-beater" model for Myxobacteria gliding: a clue for Synechococcus?

In 2007 new findings on the motors involved in gliding of *Myxococcus xanthus* were reported by (Tam *et al.,* 2007) [58]. For the general reader we recommend the perspectives article on the same issue of Science (Kearns, 2007) [36], from which we quote:

> "A tank tread-like motion of successive adhesions provides the force needed to propel a rodshaped bacterium... Mignot et al. searched for motor proteins on the inside of *Myxococcus xanthus,* a slender, rod-shaped bacterium that moves by gliding... Mathematical modeling predict that the zones of adhesion are organized on an internal helical track and that relative movement of the track could power a spiraling, corkscrew-like motion over a surface."

In fact, at David Zusman's lab at Berkeley (*http://mcb.berkeley.edu/labs/zusman/*) the motors present in this (continuously rearranging) helical structure are being identified, as well as the signalling processes. For very recent reviews, see (Mauriello, 2010) [54] and (Mauriello *et al.,* 2010 [56]. The first movie in the technical paper (Mauriello *et al.,* 2009) [53] is quite impressive. we quote form that paper:

> "We see FrzCD-GFP clusters moving in a filamentous track... Directional motility in the gliding bacterium Myxococcus xanthus requires controlled cell reversals mediated by the Frz chemosensory system. FrzCD, a cytoplasmic chemoreceptor, does not form membrane-bound polar clusters typical for most bacteria, but rather cytoplasmic clusters that appear helically arranged and span the cell length. The distribution of FrzCD in living cells was found to be dynamic: FrzCD was localized in clusters that continuously changed their size, number, and position".

Would it be possible that similar structures and mechanics will be found for *Synechococcus* swimming? George Oster (personal communication to K.E.) believes so: a similar mechanism could propagate helical waves over the surface. Kurt has a cartoon picture in his mind where all the features experimentally found could play a role, of course the crystalline S-shell to accomodate these waves, but also including the spicules. The physical and mathematical question would then be, according to amplitudes and frequencies, to determine the best mathematical modelling, by standard Stokes flows or by acoustic streaming.

To finish this section we would like to make and observation that could perhaps be of interest to microrobotic engineers. Several groups are attempting a "proof-of-concept" for robots to dispense medicines, see e.g. [100] for a recent review. In all designs that we saw, it is powered by external flagella (usually shaped in an helical pattern, sometimes as linked rods). How about bio-mimetizing the Synechococcus?

One of the authors of this essay is even ready to bet money on this: drilling translating motion will be produced if there is a rotating helical structure inside a rigid spherical body (think of a ping-pong ball filled with a viscous fluid, preferably having higher viscosity than the external medium)[32]. More generally, if the elastic properties of the external S-shell are such that that there is no transmural pressure difference, then external and internal effects are reciprocal. Externally imposed acoustic streaming can drive internal "cyclosis" [86]. More about biological cyclosis phenomena in the following discussion.

4.5. Experiments?

Would it be possible to visualize the Stokes boundary layer around a Synechococcus? Sophisticated particle imaging velocimetry is now available at micro and nanoscales. See for instance work being done at Ken Breuer's lab at Brown University (*http://fluids.engin.brown.edu/*).

A rather inexpensive "behavioral" experiment would be to observe the effect of low intensity ultrasound on the swimming pattern. Water quality firms are starting to use ultrasound to control algae invasion on lakes (*http://www.algaecontrol.us*). Low ultrasound does not kill the cells by sonoporation of external bubbles, rather by disrupting cell's gas vacuoles or other contractile organelles. A controlled experiment was done at Jiao Wen Tang's lab at Tsinghua university [88]. Some cyanobacteria suffer more than others the effect of ultrasound. Interestingly, the frequency they use is in the middle of the range of the Table 4.3.

Perhaps under a tracking microscope one could observe "herky-jerky" swimming of a single cell. According to George Hutchinson cyanobacteria "feel" an unconfortable "sense of turbulence" (Hutchinson, 2007) [33] under low intensity ultrasound. Collectively, are the majority of cells able to migrate to lower intensity regions? Is it possible to detect the "chaotic mixing atmosphere"? Related to this possibility, there is a very recent experiment by Raymond Goldstein's group (Guasto *et al.,* 2009) [30], on biflagellated algae cells[33]. See also (Leptos *et al.,* 2009) [41] and (Thiffeault and Childress, 2010) [89] for theoretical results.

Supporting evidence may come from further studies on the membrane structure and functional comparative genomics of the glycoproteins involved in motility. As we mentioned above, studies on the S-layer elasticity have begun recently. Atomic force microscopy and quantitative phase imaging are techniques that can be applied in living cells, with the aim to understand the vibration patterns. Ultimately, one would like to unravel the fine details of motion generation and kinematics of swimming. Is the rotational motion that accompanies the translation of the cell due to some helical structure being activated in the S-layer?

If our model is correct, what would be the ideal type of molecular motor for Synechococcus? It should work like a piezoelectric transducer. It turns out that one such motor, prestin, was identified in the lateral part of outer hair cells (Liberman *et al.,* 2002) [40]. Will some similar motor be found in motile cyanobacteria? Prestin is unusual as it responds instantaneously to membrane potentials (an ion channel that has lost its channel functions?). It gets its energy directly from the transmembrane electric field.

There are other features specific to cyanobacteria cells that may have an influence on the mechanics of locomotion. The S-layer has a regular network of pores reminiscent of the structures Francisco Meseguer's group has been studying for a long time, serving the purpose of acoustic lenses and attenuators. Similarly for the spicule structures, if confirmed. We described recent discoveries on the thylakoid membranes, and the special photosynthetic system that open seas cyanobacteria use. If the S-layer is shaken directly by the thylakoid membranes, the analogue for Synechococcus swimming would be the Mexican beans dance. We already mentioned gliding motility (also a hot topic). In gliding cyanobacteria, there are filamentous helical structures in the S-layer, adjacent to the muccelage pore channels, which are evidently involved in the rolling-translating motion (Read, Connell, Adams, 2007) [75] (Adams, 2001) [1].

Although it is still not clear if the mechanisms for gliding and swimming are related, we wonder about a third possibility: *acoustic levitation,* explained nontechnically in (Ueha, 2002) [90].

To conclude, we would like to discuss (in addition to the cochlear outer hair cells) three other possible biological instantiations of acoustic streaming.

- Yeast cells. Using atomic force microscopy (AFM), Andew Pelling (*http://www.pellinglab.net/*) observed that the outer membrane oscillates at between 0.8-1.6 KHz with typical amplitudes of ~3nm [66]. The magnitude of the forces at the cell wall were measured to be ~10nN indicating that they are generated by many protein motors working cooperatively. Good chemical work, Yeast! Our bread and beer say "enbuenahora"! We enjoyed Pelling's 2004 musical presentation "The dark side of the cell", done together with artist Anne Niemetz, *http://www.darksideofcell.info/docu/dsoc-doku-master.mov.* There the term "singing cells" first appeared.

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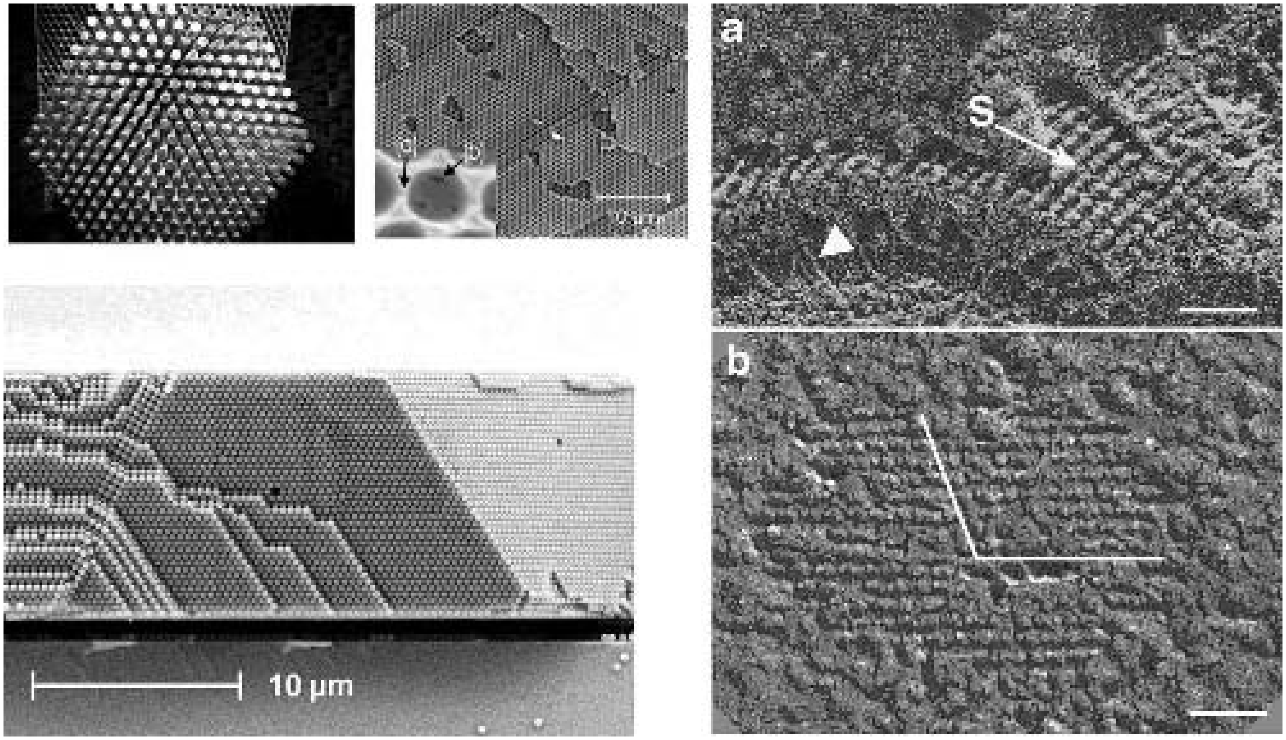

Figura 8. Left panel: Top. Sonic crystals studied in CSIC/UPV Metamaterials group. Bottom. Photonic/phononic materials studied at CSIC/ICN/UAB group. Right panel: S-layer of Synechococcus strand 8113 (Samuel et al. 2001).

- Red blood cells. Quantitative phase imaging (QFI) was used by Gabriel Popescu to detect nanoscale vibrations of the order 200 nm in red blood cells. The movie about "cell waltz" in his web site *http://light.ece.uiuc.edu/* cannot be missed (although we would prefer samba).

- Diatoms. In the tree of life, these organisms appear immediately after cyanobacteria. Diatoms are very popular among bioengineers, being basically the same size, shape and material as microchips. We speculate that they could use acoustic streaming along their raphe. See (Drum and Gordon, 2003) [19] for basic information, and the special issue on diatom nanotechnology (Gordon *et al.*, 2005) [28].

- Cyclosis. The beautiful phenomenon of organized cytoplasmic streaming was already observed in 1774 by Bonaventura Corti in cells of the aquatic plant *Nitella,* and has been studied very recently in Raymond Goldstein's lab. Current understanding is that cyclosis in plants is driven by the motor protein myosin moving along actin filaments, arranged in helical structures at the cell periphery [91]. It may be possible that acoustic streaming is also involved in cyclosis and several other biological processes in plant hydraulics [67].

5. Discussion

This final section presents in admittedly kaleidoscopical and fragmentary format, excerpts from some of the many additional sources we encountered while preparing this article. We would like to share them with the readers.

5.1. Cyanobacteria: heroes or villains of evolution?

Andrew Knoll ends his chapter *Cyanobacteria and Earth History* on Herrero and Flores, 2008) as follows:

"The cyanobacteria arguably constitute the most important group of organisms ever to appear in our planet... Their capacity to use water as an electron source in photosynthesis freed primary production from earlier limits... Their ability to couple primary production to nitrogen fixation further increased the biological carrying capacity of the oceans. And cyanobacterial production of oxygen gas transformed environments in a way that made novel physiologies and morphologies (including animals) possible. As the photosynthetic partner in the primary endosymbiotic event that introduced photoautotrophy to eukariotes, cyanobacteria contributed to the environmental transformation of land as well ad the sea. The key events in this history took place during the Archean and Proterozoic eons, but their consequences continue to shape nearly every ecosystem on Earth."

From a discussion meeting *Major steps in cell evolution* (Cavalier-Smith *et al.,* 2006) [12]:

"[The] history of life is divisible into three great ages, punctuated by the origins respectively of glycobacteria and neomura (i.e. archaebacteria plus eukaryotes), which he refers to as the glycobacterial and neomuran revolutions... The glycobacterial revolution occurred around 2.8 Gyr ago, was immediately followed by the major adaptive radiation of photosynthetic eubacteria, and led after a lag caused by the absence of the ozone layer and the huge crustal stock of reduced iron to the great oxidation event and the Palaeoproterozoic snowball Earth episodes... He argues that most protist groups underwent an explosive radiation in the Cambrian at the same time as the classical Cambrian explosion of animals and that the timing of both was set by the origins of the precursor protists such as choanoflagellates and of the first chromalveolates (eukaryotes that arose by the intracellular enslavement of a red alga, e.g. brown seaweeds) that provided novel food very soon after the ending of Neoproterozoic snowball Earth."

"Snow-ball Earth" (name coined in 1992 by Caltech geobiologist Joseph Kirschvink) are global glaciation episodes (including Rio de Janeiro). First hypothesized by Sir Douglas Mawson, the occurrence of these catastrophic events that extinguished almost all life is now generally accepted. Experts are debating fiercely about the details, but in a nutshell, too much oxygen reacting with methane in the atmosphere starts a cooling process, that feedbacks positively with the albedo effect, until the whole planet becomes totally white. The first episode, around 2.2 Gyr ago, is attributed to the cyanobacteria (did they suffered a kind of nitrous oxide narcosis?). Kirschvink asserts that lucky geological circumstances (mainly volcanic activity) allowed Earth's to warm up again that time, but it was a "close call" (perhaps Mars did not recover?) The last Snow-Ball earth episode occurred only 600 million years ago.

An article aimed to the general audience, (Kirschvink, 2005) [37] ends with a provoking thought on the opposite direction:

"Could it happen again? I remember attending a Chem 1 lecture back in a 1971 freshman class given by Harry Gray, now the Beckman Professor of Chemistry, in which he showed us a slide of the absorption spectrum of the various photosynthetic pigments. Gray, a chemist trying to find better ways of harnessing solar power, complained how inefficient the system was, because all those green photons in the middle of the spectrum were going to waste... Which leads me to think, what if some clever genetic engineer made a bacterium that could photosynthesize those green photons as well? And what if it got out and spread? If all the green photons were captured, our green planet would look black. Imagine the albedo effect of a black planet every living thing would fry. If one cyanobacterium 2.3 billion years ago could destroy most of life on Earth, it could happen again. We've got to watch those chemists."

5.2. Nature: tinkering and repeating, and great innovations

Oxygenic photosynthesis is considered by many the greatest of all evolutionary innovations. How it happened? Elsewhere in the beautiful Universe, are there other possible photosynthetic adventures? These fascinating questions were the subject of a recent discussion meeting sponsored by the Royal Society (Nisbet *et al.,* 2008) [61]. Certainly, open sea cyanobateria would benefit from being able to swim. So acoustic streaming could have been a small ingredient in that grand event (why cyanobacteria did not resort to flagella?).

Geerat Vermeij, an econo-bio-geologist from University of California at Davis, made two lists of innovations in Earth's life history, "unique" vs. "repeatable" (Vermeij, 2006) [92]. Cyanobacteria appear twice in the list of the 23 unique

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inventions, by photosynthesis and primary endosymbiosis. The other list contains first instantiations of 55 repeated innovations. His conclusions are well summarized in U.C. Davis press release (Life, the remake, Feb. 24 2006):

> "If the history of life were to play out again from the beginning, it would have a similar plot and outcomes... many traits are so advantageous under so many circumstances that you are likely to see the same things again and again... if we had an Earth-like planet, I think we'd see phenotypes and outcomes that parallel those on Earth".

We believe that acoustic streaming could be present in a revised, augmented second list. It is such a simple trick that perhaps has been unjustly underrated. Just as a curiosity, we note that "squirming" strategies have been used by Nature as a repeated "tinkering". The desert-dwelling sandfish *Scincus scincus* moves within sand in a similar fashion that a uniflagellated microorganism. Remarkably, the ratio between average tangential to normal resistance forces is close to 2, as slender body theory predicts for undulatory motion on a viscous fluid. We quote from (Maladen *et al.,* 2009) [47]:

> "High-speed x-ray imaging shows that below the surface, the lizard no longer uses limbs for propulsion but generates thrust to overcome drag by propagating an undulatory traveling wave down the body".

5.3. The flagellar motor on trial: Dover case

To our surprise, flagellar motor did not appear on either one of Vermeij's lists. See for instance this excerpt from a mini-review by Lucy Shapiro, a development biologist at Stanford (Shapiro, 1995) [81]

> "A rotating propeller at the cell surface, driven by a transmembrane proton gradient, provides many bacteria with the ability to move and thus respond to environmental signals. To acquire this powerful capability, the bacterial cell is faced with the challenge of building a tiny rotary engine at the base of the propeller... To carry out the feat of coordinating the ordered expression of about 50 genes, delivering the protein products of these genes to the construction site, and moving the correct parts to the upper floors while adhering to the design specification with a high degree of accuracy, the cell requires impressive organizational skills."

In light of this, would the flagellar motor figure in a revised first list? Care must be taken, as the above paragraph has been used by IDers (intelligent design believers) as a recognition that the flagellum is "irreducibly complex", and only the Creator could have engineered such a wonderful machine.

In fact, the flagellar motor had a key role in the Dover trial[34] (IDers lost the case). The IDers apostol (no pun intended) is Michael Behe, a biochemist at Lehigh University. Here's what he said on an interview prior to the trial:

> "What has biochemistry found that must be explained? Machines-literally, machines made of molecules. Let's look at just one example. The flagellum is an outboard motor that many bacteria use to swim... Darwin's theory is completely barren when it comes to explaining the origin of the flagellum or any other complex biochemical system."

The flagellum motor was a bad choice for an ID example. Mark Pallen and Nicholas Matzke reconstructed the phylogeny of the flagellum machinery. Their analysis is presented[35] in a recent perspective article for Nature Reviews Microbiology (Pallen and Matzke, 2006) [64]. Contrary to IDers beliefs, the flagellum is actually an excellent example of what Francisco Ayala describes as Darwin's greatest discovery: "Design without designer".

5.4. Microswimming and the emergence of cooperation

We cannot finish our essay without touching a fascinating topic, for which several new findings are appearing, and will certainly stir new controversies: the purported "social intelligence" of prokariotes. The key words "altruism", "emergence of cooperation", "quorum sensing" have precise technical meanings, and are at the root of the evolution of multicellular beings, (Wingreen and Levin, 2006) [97].

There are many evolutionary reasons that results in an advantage to an organism to move: looking for nutrients and avoiding dangerous environment are only two of the most obvious reasons. One can expect different forms of locomotion resulting from different paths in evolutionary history (convergent evolution). Moreover, in the fluid environment, the long range hydrodynamical couplings favor the appearance of collective behavior, requiring some amount of communication between the cells. This is specially visible in biofilms and concentrated suspensions.

It has been shown recently that organisms such as bi-flagellated algae cells promote fluid mixing cooperatively, and their colonies perform sophisticated dancing patterns [30]. See for instance, the movies from Raymond Goldstein's lab (*http://www.amtp.cam.ac.uk/user/gold/*). As far as we know, focused studies in this direction have not yet been done on Synechococcus samples.

We quote from a recent news release *http://www.sciencedaily.com/releases/2009/04/090420103551.htm*

> "The researchers studied the multicellular organism Volvox, which consists of approximately 1,000 cells arranged on the surface of a spherical matrix about half a millimetre in diameter. Each of the surface cells has two hair-like appendages known as flagella, whose beating propels the colony through the fluid and simultaneously makes them spin about an axis.
> Professor Raymond E. Goldstein, the Schlumberger Professor of Complex Physical Systems in the Department of Applied Mathematics and Theoretical Physics (DAMTP) and lead author of the study, said: 'These striking and unexpected results remind us not only of the grace and beauty of life, but also that remarkable phenomena can emerge from very simple ingredients.'
> The researchers found that colonies swimming near a surface can form two types of 'bound states'; the 'waltz', in which the two colonies orbit around each other like a planet circling the sun, and the 'minuet', in which the colonies oscillate back and forth as if held by an elastic band between them... These findings also have implications for clustering of colonies at the air-water interface, where these recirculating flows can enhance the probability of fertilization during the sexual phase of their life cycle."

6. Epilogue

6.1. Darwin and mathematics

In Darwin's autobiography (*http://www.gutenberg.org/etext/2010*) there is an often quoted passage:

> "I have deeply regretted that I did not proceed far enough at least to understand something of the great leading principles of mathematics, for men thus endowed seem to have an extra sense."

But why could'nt this be just an ironic recollection of his "wasted academic years", before the Beagle voyage of 1831-1836? Maybe Darwin was teasing his younger but much less adventurous cousin Galton, supposedly an expert statistician. After all, as a teenager Darwin spent his time very happily just outing and hunting. Be it as it may, we prefer a much less quoted passage, a quite opposite recollection from his childhood:

> "Looking back as well as I can at my character during my school life, the only qualities which at this period promised well for the future, were, that I had strong and diversified tastes, much zeal for whatever interested me, and a keen pleasure in understanding any complex subject or thing. I was taught Euclid by a private tutor, and I distinctly remember the intense satisfaction which the clear geometrical proofs gave me."

Mathematicians owe to Darwin at least for one big missed opportunity. Galton discouraged Darwin, as statistically nonsignificant, an experiment he was doing with a wildflower, common toadflax. Much later, R. A. Fisher (the most important bio-statistician of the 20th century) reviewed Darwin's notes, and in fact the experiment was designed in a very modern way. Galton made a blunder, and Darwin could have discovered the laws of heredity before Mendel dit it in 1866 (Rehmeyer, 2009) [76].

6.2. New opportunities

Mathematicians are *not* endowed with an extra-sense, so a preliminary disclaimer is in order. Natural selection pressures organisms to learn physics, chemistry and engineering, but mathematicians live on a Platonic universe: "Lord hath the best theorems in a small book where all proofs are elegant and perfect"[36]. This mindset makes harder the communication with "true" scientists, perhaps even harder with biologists, who deal with a sub-optimal world (hence evolution?). In fact, mathematicians seem to have (unfortunately) a good reputation among creationists. Thus we apologize to the working biologist whenever, due to a poetic license, we made inadvertently (here and there)

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an innuendo towards intelligent design. Having said that, we also apologize if, on the other side of the coin, we went overboard in an unwarranted faith in the modeling. Sir Robert May (May, 2004) [55] has well taken points on the risk of abuses in bio-mathematical modeling. For this Lighthill has some advice: learn the language. "Physical scientists must learn the meanings of the words used by the life scientists - and, of course, vice versa". This requires highly evolved scientists from both disciplines.

A new Beagle voyage is on its way 150 years after *The origin of species.* There are many opportunities for mathematicians to participate in the "post-modern darwinian synthesis" (Ayala, 2007 [3], Koonin, 2009 [39]). We refer to the issue volume of Philosophical Transactions of the Royal Society B (Biological Sciences), "The network of life: genome beginnings and evolution", compiled by Mark A. Ragan, James O. McInerney and James A. Lake (Ragan, 2009) [71].

Let us suppose Darwin's Beagle voyage could be time warped to our present. Imagine young Darwin being able to access, by internet, all the available data banks, while resting from his expeditions. We finish by listing a few of the many the opportunities for us mathematicians:

- *Networks.* The "tree of life" has been replaced by a broader concept of "network of life", due to the widespread occurrence of horizontal gene transfer.

- *Game theory.* John Maynard Smith had anticipated, and it was confirmed in controlled biological experiments that classical game theoretical situations occur at cellular and genomic levels.

- *Control and dynamical systems.* The emergence of global cooperative phenomena in large networks is one of the areas where the theory of dynamical systems has made good progress recently. Control theory is specially suited for Systems Biology. The ultimate goal would be a multiscale approach, from the genome to the working physiology of organisms.

- *Machine learning.* There is more in ML than data mining. Statistical learning theory will be instrumental in finding clues for functional phylogenetics - how Nature's innovations propagate through the network of life. All areas of mathematics are moving towards probabilistic approaches, and most likely this is how Nature overcame many NP challenges (non polynomial).

And much more... All of the core, pure mathematics, should appear in biology. Number theory and algebraic structures are essential in criptography and error correcting codes for business, why should them not be present in the DNA code? Will more Rosetta stones be found there? And, as D'Arcy-Thompson viewed, geometry and mathematical physics are everywhere.

Our colleague John Bush, a Canadian mathematician at MIT, who is a leading researcher in bio-locomotion[37] has the following motto:

> "Every imaginable physical mechanism is exploited by Nature to promote life".

6.3. Further quotes and readings

> "Wer spricht von Siegen? berstehn ist alles"
> (Rainer Maria Rilke).
> "El que resiste gana"
> (Camilo José Cela).

> "How I did enjoy shooting! But I think that I must have been half-consciously ashamed of my zeal, for I tried to persuade myself that shooting was almost an intellectual employment; it required so much skill to judge where to find most game and to hunt the dogs well...
> ... During the three years which I spent at Cambridge my time was wasted, as far as the academical studies were concerned, as completely as at Edinburgh and at school. I attempted mathematics, and even went during the summer of 1828 with a private tutor (a very dull man) to Barmouth, but I got on very slowly. The work was repugnant to me, chiefly from my not being able to see any meaning in the early steps in algebra. This impatience was very foolish, and in after years I have deeply regretted that I did not proceed far enough at least to understand something of the great leading principles of mathematics, for men thus endowed seem to have an extra sense. (Charles Darwin, Autobiography)
> "When we regard every production of nature as one which has had a long history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, in the same way as

any great mechanical invention is the summing up of the labour, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting. I speak from experience does the study of natural history become!"
"Although an organ may not have been originally formed for some special purpose, if it now serves for this end we are justified in saying that it is specially contrived for it. On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for that purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms."

(Charles Darwin, On the origin of species, 1859)

We end this essay with the question: Is there a conflict of evolution with a true religious belief?

> "The hearing ear, and the seeing eye, the LORD hath made even both of them"
> (Proverbs 20:12).

With due humility, we refer to Francisco José Ayala's (*Darwin And Intelligent Design*, 2006) [4] book.

The provocative lines about biology and ethics by Fernando Savater in (*El contenido de la felicidad, 1986,* [79]) took us to Ernst Mayr 1999 Crafoord prize lecture *Darwin's Influence on Modern Thought.* Mayr tells us that ultimately, Darwin wanted to provide a scientific foundation for *ethics,* the singular evolutionary innovation by humans.

All our genes say: "Give Peace a chance!" Let it be.

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NOTES

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1 *http://www.ibvf.cartuja.csic.es.* The school of Spanish biochemists of Manuel Losada is giving important contributions to bioenergetics and nitrogen fixation.

2 See the podcast in *http://explorations.ucsd.edu/Features/2008/Green_Bullet.*

3 Two of us (KE and JK) fear having witnessed those events like "Forest Gumps". We became aware of this two findings already in the mid 1990's, but only recently we started to read more about both subjects.

4 In fact, there are many locomotion strategies in microbiology awaiting mathematical modeling, see eg. (Bardy *et al.*, 2008) [6], (Jarrel *et al.*, 2008) [35].

5 Rayleigh made a note in the second volume of his celebrated *Theory of Sound* (Rayleigh, 1896) [72]. An analysis of Kundt's tubes appeared in (Rayleigh, 1883) [73].

6 *http://www.cin2.es/english/research_groups.php.*
See the summary in *http://nanocat.uab.cat/dataeng/recerca/phopriv/pho_research.php.*

7 *http://www.metamaterials.ctfama.org/*, see the images and description of their results.

8 Spain's nanotechnology network web page is *http://www.nanospain.org/nanospain.htm.*

9 After a long dormant period, Nyborg (and others) revived acoustic streaming in the 1950's. Emeritus professor at the University of Vermont, as this article was being written a special commemoration for this 50th year was about to happen: *http://www.uvm.edu/~physics/e-news/#Nyborg.* For a recent techni-

cal article on medical ultrasound see (Wu and Nyborg, 2008) [99].

10 Specially the "shrimpoluminescence" page, *http:// pof.tnw.utwente.nl/3_research/3_t_shrimp.html.* There is also a BBC Weird Nature feature (see the video on YouTube).

11 The sequel was not completed. Lighthill died in 1998, at 74. While doing his 5th swim around the English Channel island of Sark, Australia, it seems that he suffered a heart attack and drowned.

12 *http://www.acoustics.org/press/136th/meseg2.htm*

13 The fossil record indicates that these bones evolved from the jaw bones of ancient reptiles that had much cruder auditory systems. These ancient reptiles sensed ground vibrations through the bones in their jaws. A transition fossil was recently discovered in China by Zhe-Xi Lao of the Carnegie Museum of Natural History at Pittsburgh. The ancient mammal *Yanoconodon allini* has three ossicles bones that, unlike modern mammals, are connected to the bones of the jaw by a bone not found in modern mammals. This mammal retained the ability to sense ground vibrations through its jaw (Biello, 2007) [11]. The amniote cochlear philogeny has been reconstructed in (Manley, 2000) [48]. It has been speculated that the outer hair cells evolved from tunicates (Caicci *et al.*, 2007) [13].

14 There is a 106 million dollar prize for finding the best mathematical arena for this equation *http://www.claymath.org/millennium/Navier_StokesEquations/.*

15 Vivid illustrations of rectification are motions of cell phones on a table when set in vibratory mode.

16 For a general introduction to control theory, see (Fernandez-Cara and Zuazua, 2007) [22]; for the technological state of the art see Richard Murray's Caltech webpage *http://www.cds.caltech.edu/~murray/cdspanel/.*

17 CSIC sponsors the scientific journal Geometric Mechanics *http://aimsciences.org/journals/jgm/index.htm,* and several activities of the research network *http://www.gmcnetwork.org/.*

18 His thesis, filed in 1995, was supervised by Richard White with the help of Roger Howe. After his Ph.D., Moroney went to work in industry. Howe moved a few years ago to Stanford. White is now emeritus professor in Berkeley where he directs the Sensor and Actuator Center.

19 Nanosystems Initiative Munich, *http://www.nano_initiative_munich.de/.*

20 *http://www.physik.uni-augsburg.de/.* Media, intriguing videos and nontechnical material can be seen at *http://www.advalytix.com/mixing_1343.htm.*

21 *http://www.eng.monash.edu/non-cms/mnrl/home.html.*

22 Now scientist emeritus, *http://www.whoi.edu/profile/jwaterbury/*

23 Jay McCarren Ph.D. thesis can be downloaded from *http://openwetware.org/wiki/JayMcCarren.*

24 *http://www.nature.com/nature/journal/v424/n6952/abs/nature01943.html.* For details on the genome, *http://genome.jgi-psf.org/synw8/synw8.home.html.*

25 For information on the competitor of Synechococcus among the ocean cyanobacteria, see *http://rocaplab.ocean.washington.edu/research/cyanobacterialgenomics.* Palenik asserts that Synechococcus is more "generalist".

26 See also the note *http:// www.sciencedaily.com/releases/2008/02/080221152009.htm*

27 *http://www.rowland.harvard.edu/labs/bacteria/.* There one can also find a Physics Today 2000 review about flagellar locomotion. For a 2008 update, see (Berg, 2008) [9].

28 For the non initiated: (KE) was just following the steps (rather the crawl strokes), of the famous mathematician Stephen Smale, probably the most influential mathematician of our times. Smale attributes to the beaches of Rio the inspiration for a couple of his most important discoveries (Smale, 1998) [83].

29 George Oster (*http://www.cnr.berkeley.edu/goster/home.html*) is certainly one of the most influential bio-mathematicians. A congress commemorating his 60th birthday was held this year at Berkeley, *http://www.math.ucdavis.edu/ mogilner/Berkeley.html.* A profile on his work appeared in PNAS, *http://www.pnas.org/content/103/6/1672.full.*

30 Molecular motors are special proteins that by doing conformation changes can carry cargo along microtubules (tracks for the intracellular "railroad system"). Molecular motors acting in unison, controled by the cell's genetically constructed "software", are responsible for all types of cell movement. For this fascinating subject, we refer to outreach articles by Ricardo Arias, a young CSIC investigator from Centro Nacional de Biotecnologia, see *http://www.cnb.csic.es/~jrarias.*

31 Possibly also with phononic/photonic to enhance the effects, but for now we prefer not to speculate too much.

32 The other authors disagree with J.K.. The minority argument is essentially the same as that given by (Purcell, 1997, a the posthumously published paper) [70]. Just make the propeller inside rather than outside.

33 We urge the reader to look at the movies *http://www.haverford.edu/physics/Gollub/SwimminMicroorganisms.*

34 There is detailed information in wikipedia about the Tammy Kitzmiller, *et al.* v. Dover Area School District, *et al.,* Case No. 04cv2688.

35 See the video *http://www.youtube.com/watch?v = SdwTwNPyR9w*

36 Attributed to the hungarian mathematician Paul Erdos. He also said: "You don't have to believe in God, but you should believe in the Book".

37 *http://math.mit.edu/~bush/.* John is also a good friend of Spain and Brazil. One of us (JK) had the privilege to share with him a minicourses in the Mathematics for Peace and Development summer school, Cordoba, 2006, *www.uco.es/congresos/mpd,* a satellite event of the (*www.icm2006.org/*).

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