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A Tour of My Soft Matter Garden: From Shining Globules and Soap Bubbles to Cell Aggregates

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Abstract

Like *The Magic Flute*, my career has been paved by wonderful and unexpected stories played by enthusiastic and talented students, in close contact with experiments and industry. I participated in the birth of soft matter physics under the impulse of Pierre-Gilles de Gennes: polymers, liquid crystals, colloids, and wetting, which I later applied to the study of living matter. By teaching in the early days at the Institut Universitaire de Technologies d'Orsay, I came into contact with industry, which gave me the chance to collaborate with several companies: Rhône-Poulenc, Dior, Saint-Gobain, Rhodia, and Michelin. These partners have not only largely financed my research in physical chemistry but they also offered a wealth of innovative research topics. In 1996, when Professor Jacques Prost became the director of the Physico-Chimie Curie laboratory, in the Pavillon Curie built for Marie Curie, I turned to biophysics. I initiated collaborations with biologists, applying soft matter physics to the mechanics of cells and tissues. Pierre-Gilles de Gennes has been a wonderful guide throughout this scientific adventure to build my soft matter garden.

1. CHILDHOOD IN ANNECY

I need to begin this autobiography by describing my childhood and my parents (**Figure 1**), who have been models of life teaching to their five children to be strong and simple and to get to the bottom of things without fanfare. In March 2016, I was made "Officier de la Légion d'Honneur" by Professor Yves Quéré, from Ecole Polytechnique. He summarized beautifully my origins:

> What parents you had! Pierre Wyart, your father, whose own father was driving locomotives to the North Railroad Company, and whose brother, Jean Wyart, was the famous mineralogist and crystallographer; some of us were able to attend his classes at the Sorbonne. Your father started the Ecole Polytechnique at 17 years old in 1928, magnificently illustrating how one could climb the French social ladder of the time–not so blocked! His undergraduate studies were soon after interrupted by tuberculosis, which penetrated the vertebrae. He therefore entered in a sanatorium in Briançon where he stayed for 5 years. Dura calamitas for this young man full of ardor, vitality and desire to undertake, but also felix calamitas since it is there, in the sanatorium of Briançon, that he met his future wife, Liliane Weber, your mother. Finally, he recovered and entered a School of Application in Saint Etienne where he learns hydraulics before being named in Annecy. It is during that time that you are born, on Sept 11th, 1944. The family now lives in the small town of Verrier du Lac, where you were a pupil in a single-class school. During these years, you have a lot of fun with the children of the neighboring farms. So much fun that when the family has to leave to go to Annecy where you were already enrolled in primary school, you burst into tears and repeat a class: bad luck for Françoise that worries her parents until she passes the sixth-grade exam, her first intellectual high. Back to her father: in 1946, Pierre Wyart participated in the creation of nothing less than the company Electricity of France, which he quickly climbed the ladder, a company that he will even be proposed to become the general director. To the highest functions this man of intelligence, action and dialogue, a sort of Julien Sorel of modern

Figure 1

Liliane and Pierre Wyart at the Electricity of France dam in La Girotte. View of Mont Blanc from the early childhood of Françoise Brochard-Wyart. Photo provided from the author's private collection.

times, will never forget that he is the son of a worker. Always active and full of energy, when he retires, he creates and leads an agency dedicated to the resolution of international conflicts on energy. Your mother was an amazing woman, full of energy and vision, who wished to be a doctor but she was born a little too early: studies are for men, so she became a nurse. Your mother, who became a nurse traveling to Northern African countries such as Algeria, from where, anticonformist as she was, she brought back a monkey and an antelope and moved to Briançon's hospital, where she met a charming young man suffering from tuberculosis. . . Raising her 5 children, your mother practiced throughout her life the taste for culture (she managed libraries in old people homes) and openness to others, receiving at home young refugees and isolated elderly. She died in the summer of year 2000, with your father following her less than two months after, crushed with grief.

The young Françoise was a brilliant student who was born at the end of the Second World War and had the opportunity, that her mother did not have, to complete her education. After high school, Françoise went to the Ecole Normale Supérieure (ENS) Cachan in 1964 and passed her aggregation of physics in 1968, an unusual year to prepare such a hard exam! In the same year, she started her Ph.D. in the Solid State Physics laboratory in Orsay.

2. ORSAY 1968–1977

Two years after my admission in ENS Cachan, I enrolled in 1966 in the master of Solid State Physics where classes were instructed by notorious professors such as J. Friedel, A. Guinier, P. Nozières, and Pierre-Gilles de Gennes (hereafter referred to as PGG) (**Figure 2**). Together, these great minds conveyed a novel, personal, and exciting vision of physics. After passing the

Figure 2

Françoise Brochard-Wyart and Pierre-Gilles de Gennes at Sanary in 1991. Photo provided from the author's private collection.

Aggregation of Physics, I joined the Laboratory of Solid State Physics (Orsay) to prepare a PhD under the supervision of PGG. After the events of May 1968, one could not enroll for a PhD without a permanent position. Consequently, we were very few PhD students! For my part, I received a permanent assistant professor position in the fall of 1968 at University Paris XI, so I started to teach and do research while soon taking care of my first child, Pascale, born in October 1968, who was soon followed by my first son, Virgile.

After some brief work on superconductivity under the supervision of Fyl Pincus, I joined the Liquid Crystal Group as a theorist to work in close collaboration with several experimental teams led by Etienne Guyon, my former professor at ENS Cachan, who was key in building up my confidence; Georges Durand; Madeleine Veyssié; Robert B. Meyer; and PhDs Francis Rondelez and Pawel Pieranski. My colleague Liliane Léger introduced me to her beautiful experiments as we performed twin PhDs, hers in experimental physics and mine in theory.

Nematic liquid crystals are very sensitive to external fields. At the time I was working on my PhD, it was interesting and important to understand the transient responses of nematic liquid crystals to suddenly applied magnetic or electrical fields. I therefore studied the dynamics of the Fredericks transition of a nematic liquid crystal. The nematic is aligned by the surfaces of the sample and distorted by a magnetic field perpendicular to the nematic orientation. A distortion is observed above a threshold field H_c (1, 2). I studied the hydrodynamic "back flows" (3) induced by the rotation of the molecules. For a given field $H > H_c$, the system may choose between two different distortion patterns, and the nematic slab breaks into domains. I analyzed the structure of the walls separating two domains and showed that the thickness of the wall diverges at H_c. I modeled the motion of the domain and the slowing down of the dynamics near the critical magnetic field (4). This project was a first step toward studying the dynamics of liquid crystal phase transitions. The different types of liquid crystals are indeed connected by remarkable transitions: Critical fluctuations much subtler than those of the usual systems (liquid–gas, magnetic. . .) appear at these transitions. My background in superconductivity became very useful in this area, as certain transitions, like smectic A/nematic or smectic C/A, resemble each other from the point of view of their symmetry superfluid transitions. Therefore, I built dynamic scaling laws (5–7) in analogy with the models of Halperin and Hohenberg. This work, which made up most of my PhD thesis, was done in collaboration with several groups in Orsay.

At the end of my PhD, we extended these works to lipid-water mixtures, referred to as lyotropic liquid crystal. We calculated the collective modes of lamellar phases and found six classical modes of thermotropic smectics, and an additional mode, the slippage mode, due to the addition of one variable, the lipid concentration (8). This seventh mode was later observed at Harvard University by forced Rayleigh diffusion (9). I defended my thesis in 1974 with the title "Dynamic Properties of Mesomorphs."

At that time, PGG put me in contact with Jean-François Lennon, a researcher from the Laboratory of Hematology from the Pasteur Institute, who carried out the first quantitative studies on the scintillation of red blood cells, a strange phenomenon observed for a long time in phase contrast microscopy but which was totally unexplained at the time. The flicker of the red blood cell was believed to be caused by active movement of the cell, at a physiological frequency related to the life of the cell, like heartbeats. We embarked on a nice collaboration to understand this phenomenon. Suddenly, the walls of my office in Orsay became decorated by the experimental data of Lennon. He measured experimentally the correlation functions for the flicker intensities at two different points on the cell surface at various filtering frequencies. We interpreted theoretically these results in terms of the thermal fluctuations of the thickness of the biconcave cell shown in **Figure 3**, which modulates the transmitted light. In physiological conditions, the membrane surface tension vanishes, and the resistance to deformation is mainly due to curvature energy. In

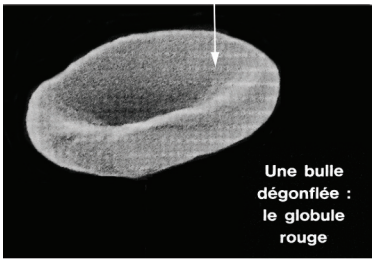

Figure 3

Biconcave shape of a red blood cell modeled as a deflated bubble. Reproduced from Reference 11. Copyright (1977), *La Recherche*.

this approximation, the fluctuations are of very large amplitude (a fraction of a micron) as expected according to the observations. The detailed shape of the correlation functions is in rather good agreement with the theory (10). We conclude that a purely physical model is sufficient to interpret the flicker effect, but that rather stringent physiological conditions are required to maintain the zero-surface tension, which is critical to the effect. This early work was crucial for my transition to biophysics many years later!

The period after the events of May 1968 was a period of doubt for scientists of my generation who were in search of meaning. Some became physicians or moved to farms raising sheep in remote areas such as the plateau of Larzac in the south of France. For my part, after completing my PhD in 1974, in order to experience the life of a scientific editor, I wrote an article for the public journal *La Recherche* (**Figure 3**) (11), but I did not like the experience, so I decided to stay in academic research.

3. COLLEGE DE FRANCE 1977–1985

PGG had been nominated in 1971 as Professor for the Chair of Physics of Condensed Matter in College de France. In 1977, I joined his laboratory, where I found some of my old friends from Orsay, Veyssié, Léger, and Rondelez. That same year, my daughter Claire was born, and in 1978, my son Matthieu followed. I took part in the fast evolution of polymer physics, initiated by PGG with Gerard Jannink and Jacques des Cloiseaux. The famous theorem "$n = 0$" of PGG in 1972[1] was a revolution in polymer physics, where suddenly all the theoretical techniques developed for critical phenomena replaced mean field approaches. The scaling laws were visualized by PGG, who introduced the picture of blobs, a statistical object to characterize the monomer–monomer correlations.

When I decided to study the physics of polymers, my previous training in hydrodynamics and phase transitions became extremely useful. My first calculation in polymers was to transpose the physics of polymer solutions in 3D to 1D, where polymers are confined to capillaries.

[1]This theorem is presented by PGG in his Notice de titres et travaux (1978) (author's private archives). "On the theoretical level, it has been possible to establish a rigorous relation between the statistics of the chains and the transitions of phase. This relation is quite abstract: it is to study a magnetic system whose magnetization possesses independent elements and to pass to the (nonphysical) case where $n = 0$. However, we know, from many examples in theoretical physics, that the extension of some results to nonphysical values of the parameters can be fruitful (as well as complex angular moments in collision physics). The '$n = 0$ theorem,' established by us in 1972, has made it possible to transpose the enormous theoretical arsenal accumulated with regard to phase transitions to polymer problems. Thanks to the $n = 0$ theorem, the problems related to self-avoiding random walks have been fundamentally related to the physics of phase transitions, all of them having a very great universality, that is, laws independent of the local structure."

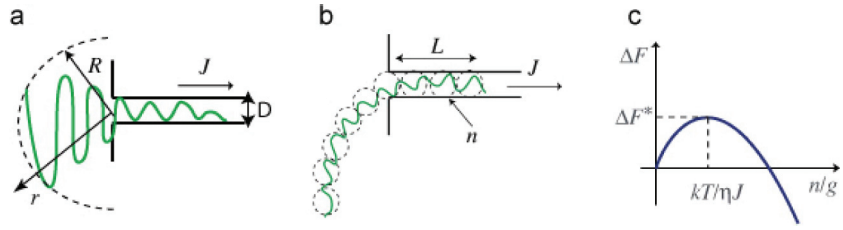

Figure 4

Forced passage of a flexible polymer chain under strong flows: (*a*) affine deformation, (*b*) suction, and (*c*) free energy of the chain versus the number of monomers sucked in the capillary. Adapted from Reference 13 with permission. Copyright (1978), American Chemical Society.

3.1. Polymers Confined in a Pore

An interesting problem that is important for enhanced oil recovery is the dynamic behavior of polymeric chains trapped in very fine pores. I constructed dynamic scaling laws for these problems (12), which PGG was proud to claim disproved a previous Debye analysis.

Subsequently, I worked closely with S. Daoudi on the forced passage of one single polymer chain through the entry of a pore and on the behavior of polymer solutions in convergent/divergent pores (13). The two mechanisms shown in **Figure 4** are an affine deformation under convergent flows at the entry of the pore and a suction of the polymer by the flow of solvent inside the pore. They both give the same threshold flow for the passage of the polymer. The experiments were carried out in the following years by a collaborative effort of researchers from the French Institute of Petroleum (G. Chauveteau) and the College of France (Rondelez and Léger).

Later on, I studied the properties of melted polymer mixtures in confined geometry (14) that was part of E. Raphaël's thesis. More recently, with C. Gay and T. Sakaue, we studied the passage of branched polymers and showed that the forced penetration into a pore does not select the chains according to their length or their topology (15, 16).

3.2. Polymers in Solution

For a long time, polymer solutions were described by a mean field theory developed by Flory & Huggins (17). This approach was not able to interpret a number of anomalous exponents measured by neutron scattering. The theory of polymers in good solvent had progressed enormously from the analogy with phase transitions (18). I used these scaling approaches to study polymers in a variety of solvents.

3.2.1. Polymers in bad solvents. With PGG, I studied the movements of a chain in bad solvent where it is strongly folded on itself and where it forms many self-nodes (19). This aspect, ignored in classical literature, leads to curious effects observed by neutron and light scattering (20, 21) which do not follow simple dynamical scaling laws because there are two characteristic lengths, the monomer–monomer correlation length and the distance between the nodes (22).

We then studied the dynamics of swelling of a polymer droplet immersed in a good solvent, where we introduced the "magic length." Polymer dissolution is a significant problem for many industrial processes, with a lot of empirical data available but without an overall view. We have been able to analyze different steps in the process and have shown on a practical level that there is an optimum size for the concentrated polymer drops that must be prepared (by mechanical

stirring) before starting the true dissolution: The time of dissolution decreases with the size of the droplets, but it reaches a plateau value because the chains have to disentangle.

We also studied later with C. Williams the dynamics of collapse of one single chain (23) and the swelling of a gel with free polymer chains (24).

3.2.2. Polymers in liquid crystal solvents. I followed Veyssié and J. Dubault's experimental work on the usual polymer–liquid crystals mixtures. I modified my first description, which was limited to weak coupling situations. Quite often, the nematic order is completely destroyed inside the chain and one has a strong coupling situation: isotropic solvent droplets in the region of the cloud of monomers. For short chains (smaller than the coherence length ξ of the nematic), the unexpected result is an "ideal" chain behavior. For long chains ($R > \xi$), there is a "collapsed" regime. I also calculated the phase diagram of nematic polymer mixtures with P. Levinson (25).

3.2.3. Dynamics of polymer melt. Couplings of melt-compatible polymers are rare, but they are of great importance for industrial applications (polymer metallurgy, self-adhesion). For such couplings, I had predicted unusual interdiffusion laws (26). Following a collaboration with experimenters R.L. Laurence (Amherst), J. Klein (Cambridge), and E. Kramer (Cornell), it turned out that my results explained the interdiffusion in the case of comparable lengths, but did not apply to the case of asymmetrical junctions.

My first theoretical interpretation, based on the model of reptation of polymer chains crawling in fixed "tubes," was incorrect for the case in which one of the species is much shorter than the other. It took me five years to arrive at a satisfactory theoretical description, in which the tubes themselves move with a velocity unambiguously determined by a balance of forces on the tube (27). The small chains swell the transient network of the long chains. I was very proud of this result, but I published it in French in the *Comptes rendus de l'Académie des sciences* (Paris): Masao Doi, who was at first skeptical to the motion of tubes, recognized its importance, used it, and asked me to put my name in his article because my own article would be lost and overwhelmed in that journal.

3.3. Polymers at Interfaces: Role of Connectors

The graft polymers are used as connectors (example: metal/polymer adhesion), as colloid stabilizers (for example, Indian ink, "hairy" vesicles formed of partially water-soluble lipids and copolymers, which stand two days in blood, while simple vesicles are instantly destroyed), and as wetting control agents (for example, silanized silicon wafers). These long graft chains also play an important role in the rheology of polymers at interfaces, which was studied at the College by Léger and Hubert Hervet. A polymer melt slides on a smooth surface. On a surface onto which a few chains have been grafted, the slip is destroyed at low shear rates because of the strong friction but restored at high shear rates because the chains undergo a coil-stretch transition and disentangle with the melt. PGG and I introduced the concept of a marginal state for a wide range of sliding velocities (four decades), in which friction becomes solid type (28). We extended this study to the slip of a rubber on a grafted surface, mainly with Ludwig Leibler, Armand Ajdari, and Gay. It's amazing that a marginal state has been observed recently in the shearing of entangled fire ants glued to the wall of the rheometer with Velcro!

I also participated in the development of a theoretical model of brush-rubber adhesion. This was later extended to cellular adhesion induced by specific binders (29) and its measurement by an enforced cell's detachment.

3.4. Wetting

The physics of wetting was initiated at the Collège de France thanks to the French Institute of Petroleum. They were concerned with the wettability of rocks and the role of polymers used in oil recovery.

The different regimes of wetting of a droplet deposited on a substrate (partial versus complete wetting) depend upon the sign of the spreading parameter *S*. For the case of complete wetting (*S* positive), the structure and the dynamics of the precursor film, named van der Waals pancake, was studied by Jean-François Joanny, who at this time was a young student of PGG's. I decided to extend their work to the wetting of fibers with two PhD students, David Quéré and Jean-Marc Di Meglio.

If the spreading on a solid plane was relatively well understood, the spreading on fibers (textiles, fiberglass, carbon, hair) remained mysterious. Why does a drop spreading on a plane no longer spread on a fiber? We have shown that in this situation, the excess liquid–gas interface linked to the cylindrical geometry leads to a new situation, which we named pseudopartial wetting (30): The drop does not spread even if *S* is positive! The equilibrium state is a droplet in coexistence with a microscopic film. We predicted droplet-manchon transitions and studied the dynamical properties of the spreading: A drop placed on a fiber spreads by emitting two films of microscopic thickness. We also studied the stability of films deposited on a fiber (31), the threshold thickness beyond which the liquid sheath splits into droplets, and the dynamics of this Rayleigh instability (**Figure 5**). This work is crucial for the coating of textile fibers: During the extrusion of the polymer wire at gigantic speeds over the Earth-Moon distance, the fiber must be covered with a lubricating liquid film. Any fault causes a break in the fiber, and the coil becomes entangled. Visiting L'Oréal, I discovered that they used our work for the formulation of mascara: The drying must be faster than the rise time of the instability to get a regular coating of the cilia.

We have also investigated the wetting phase diagram of solid substrates coated with a molecular film (32). Comparing the polarizability of the film versus the polarizability of the solid, we predicted complete, partial, and pseudopartial wetting for the case of a low-polarizability solid (plastic) covered with a polarizable layer (gold). A sessile droplet spreads on gold but does not spread on golden plastic: At equilibrium a macroscopic droplet with a finite contact angle coexists with a nanoscopic precursor film.

At the end of my stay at the Collège de France, I attended PGG's lecture on soap films. He described the growth of Newton black films observed by K. Mysels, which nucleate during the drainage of a vertical soap film. For fun, I transposed the theory that PGG described for suspended

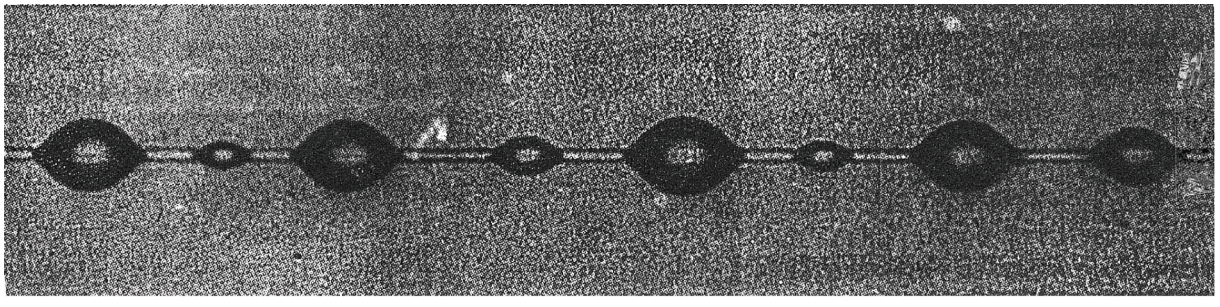

Figure 5

Instability of liquid films on fibers: an enlarged view of beaded thread. Figure adapted from Reference 31 with permission. Copyright (1990), The American Association for the Advancement of Science.

films to the case of films supported by a solid substrate. A black film becomes a dry patch that opens up on a wet substrate. Dewetting was born, and it was going to keep me busy for almost 10 years! I can see dewetting every day in my shower when a dry region opens on my wet skin. This was around 1984, when my son Olivier was born.

4. SORBONNE UNIVERSITY 1986–1991

In 1986, I was appointed Professor at Paris VI. With J.P. Badiali, M.P. Pileni, and Rondelez, we created a team focused on the problems of structure and reactivity at interfaces in the laboratory of Physical Chemistry, in the Jean Perrin building. In this new environment, I tried to keep the same style of work, dealing with various areas of physical chemistry (surfactants, polymers, hydrodynamics), and following fairly closely industrial needs (textile, petroleum, cosmetic industries, chemical engineering). We started to work on wetting and dewetting; PhD student Claude Redon was financed by Dior: "We want to produce a shampoo to keep our hair dry when going to the pool!" We did not succeed in achieving what nature has been able to do for the feathers of ducks, which remain dry thanks to nanoparticles that make them super hydrophobic, but we started the first fundamental studies of dewetting by nucleation and growth of a dry patch (33) and spinodal decomposition (34). We monitored and modeled the dynamics in both viscous and inertial regimes, in which capillary waves are induced by the motion of the rim collecting the liquid of the dry region (35). Wetting is a science that seduced me because it intervenes in our daily life. On the aesthetic level, the experiences are very beautiful but not as simple as they seem! Wetting also leads to many industrial processes, as illustrated in our book, *Capillarity and Wetting Phenomena*, with PGG and D. Quéré (36). This direction of research gave me the opportunity to work with Dior, Atochem, Rhône-Poulenc, Michelin, Valéo, and Airbus.

Thanks to Rondelez, I became interested in phase transition in Langmuir monolayers. With D. Andelman and Joanny, I have shown that the interactions between permanent dipoles modify the phase diagram (37): At the liquid–gas or liquid–liquid/condensed liquid transitions, long-range repulsions between dipoles give rise to periodic super crystal arrangements visualized directly by epifluorescence.

When the team moved to Jussieu in 1991, we decided with Rondelez to join the Curie Institute in the section of Physics directed by Monique Pagès, which was changing orientation toward soft matter. That same year, my son Marc was born.

5. INSTITUT CURIE 1991–PRESENT

In 1992, I entered the Physics and Chemistry section of the Institute Curie where I founded, with Rondelez and Didier Chatenay, the team Physics of Surfaces and Interfaces. In 1996, Jacques Prost brought our team and a team of chemists together to create the PCC, i.e., the Physico-Chimie Curie Unit. It lies at the interface between physical chemistry and cell biology. I started the team Surface Douces (Soft Surfaces) focused on hydrodynamics and polymers at interfaces, with outstanding experimentalist Axel Buguin, and a great time started for me!

In the 2000s, I began a gradual transition from soft matter to biology by studying biomimetic systems. Then we validated our approaches on cells, which raised new questions that I developed with my team and in collaboration with groups in France and abroad. My experience with polymers was useful because the cells, from a mechanical point of view, can be considered as viscoelastic jelly beads surrounded by a liquid membrane that gives them a surface tension, like droplets. This was around 2003, when I was nominated a member of the University Institute of France.

5.1. Soft Matter 1992–2008

During these years, I pursued activity in soft matter and developed new projects in biology.

5.1.1. Dewetting at soft interfaces: aquaplaning and cellular adhesion. On the problem of adhesion, we started a long-term program with Michelin to investigate rubber/wet surface contacts. We first studied theoretically (38) the dynamics of dewetting of a liquid film intercalated between soft rubber and a rigid substrate. Using reflection interference contrast microscopy, Pascal Martin was able to follow the dynamics of growth of dry adhesive contacts. Buguin built a macro atomic force microscope in which the tip is replaced by a millimetric elastic ball, and we studied the adhesion and the friction of rubber beads pressed on a rigid plate in air or immersed in a liquid. When the plate slides at a velocity U larger than a threshold velocity, the contact is lubricated, corresponding to the aquaplaning that happens when a car loses control on a wet road (**Figure 6*a***). However, if the sliding surface carries an asperity, a dry wake can be induced (**Figure 6*b***), in analogy with Cherenkov radiation, with a Mach angle derived from competition between the dewetting velocity V and the invasion velocity U (39), which restores adhesion. We used the same setup to study cellular adhesion (40, 41), which is also done by the elimination of a liquid film of comparable thickness. After having worked on model systems (an elastomer ball immersed in a viscous liquid and sliding on smooth glass), adhesion was studied on systems closer to reality: (*a*) microstructured surfaces (pillars) (**Figure 6*c***) to simulate the asperities of the soil and

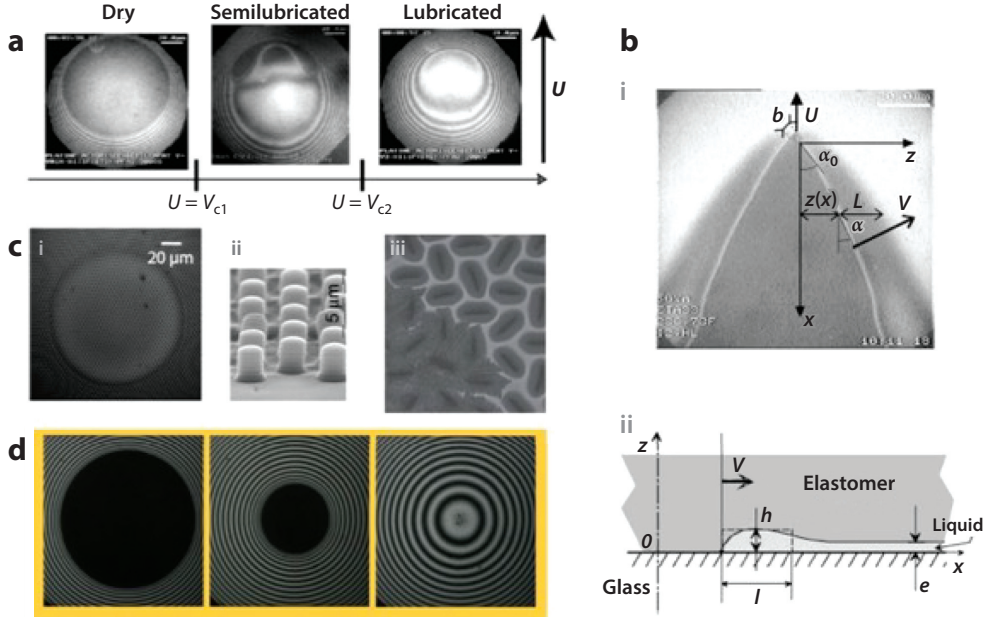

Figure 6

(*a*) Aquaplaning: sliding of an adhesive rubber-glass contact immersed in a liquid versus the sliding velocity U: dry, semilubricated, and lubricated regimes. (*b*) Cherenkov dewetting: (*i*) Mach angle and (*ii*) profile of the rim collecting the liquid. (*c*) Suspended contact of a soft bead on a microstructured substrate (*left*) made of pillars (*middle*), and instability of an antifrost polymer film exposed to a moist atmosphere (*right*). (*d*) Progression, from left to right, of the detachment of a soft bead adhering on smooth glass. Panel *a* adapted from Reference 42. Panel *b* adapted with permission from Reference 39. Copyright EDP Sciences, 2002. Panel *c*, subpanels *i* and *ii*, adapted from Reference 43. Panel *c*, subpanel *iii*, adapted from Reference 44. Panel *d* adapted from Reference 45.

(*b*) high speed friction. These projects required micro-fabrications of surfaces and the realization of a rotating disk force machine to explore very high-speed ranges.

In addition, we built biomimetic models of cells at all scales, ranging from millimeters to microns: viscoelastic beads decorated with proteins to simulate the properties of the cytoskeleton and specific adhesion, soft shells to represent the cortex, and suction cups for simulating the adhesion of amoebae in the intestine. These giant systems allowed us to more easily study the dynamics of adhesion and detachment on smooth (**Figure 6*d***) and rough surfaces (46).

5.1.2. Bursting of viscous bubbles. We are in 1991, when PGG receives the Nobel Prize. Rhône-Poulenc offers us a box in plastic containing a magic paste with the inscription "la matière molle: vous connaissez?" This paste has kept all its properties: rolled in a small ball, it bounces at short times, and it spreads like a liquid. Playing with this paste to make a thin film, I saw the formation of holes.

For a hundred years, physicists (Dupré, Rayleigh, . . .) have been passionate about understanding the bursting of soap films; G. Debrégeas is the first to have made films of viscous polymers without surfactants and studied their bursting (**Figure 7**), which gives new laws: The inertia is negligible, and the viscoelastic properties of the film control its rupture, which is as fast as the bursting of soap bubbles, because of the radial plug flows that give rise to a very small viscous dissipation (47, 48).

5.1.3. Hydrodynamic extrusion of membranes tubes. A hydrodynamic probe was developed by O. Rossier based on the extrusion of membrane tubes from giant vesicles (49). A vesicle is attached to a microstick and submitted to a flow (**Figure 8*a***). A tube is extruded above a threshold force f_0, at which we have coexistence between a spherical vesicle and a membrane tether. We modeled this transition in analogy to the unbinding of a polymer chain in a bad solvent. Nicolas Borghi applied the tube hydrodynamic extrusion to test the properties of cell membranes (**Figure 8*b***) and the adhesion of the plasma membrane to the cytoskeleton (50, 51). We modeled

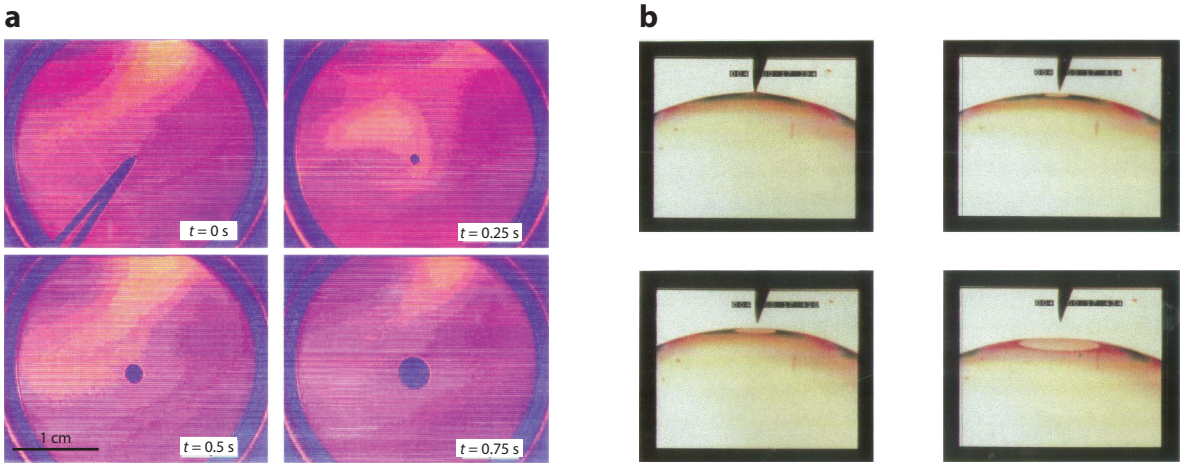

Figure 7

(*a*) Bursting of a flat, suspended, ultraviscous film punctured with a needle. (*b*) Bursting of a viscous bubble obtained by injecting air in an ultraviscous polymer melt. Panel *a* adapted with permission from Reference 47. Copyright (1995), American Physical Society. Panel *b* adapted with permission from Reference 48. Copyright (1998), The American Association for the Advancement of Science.

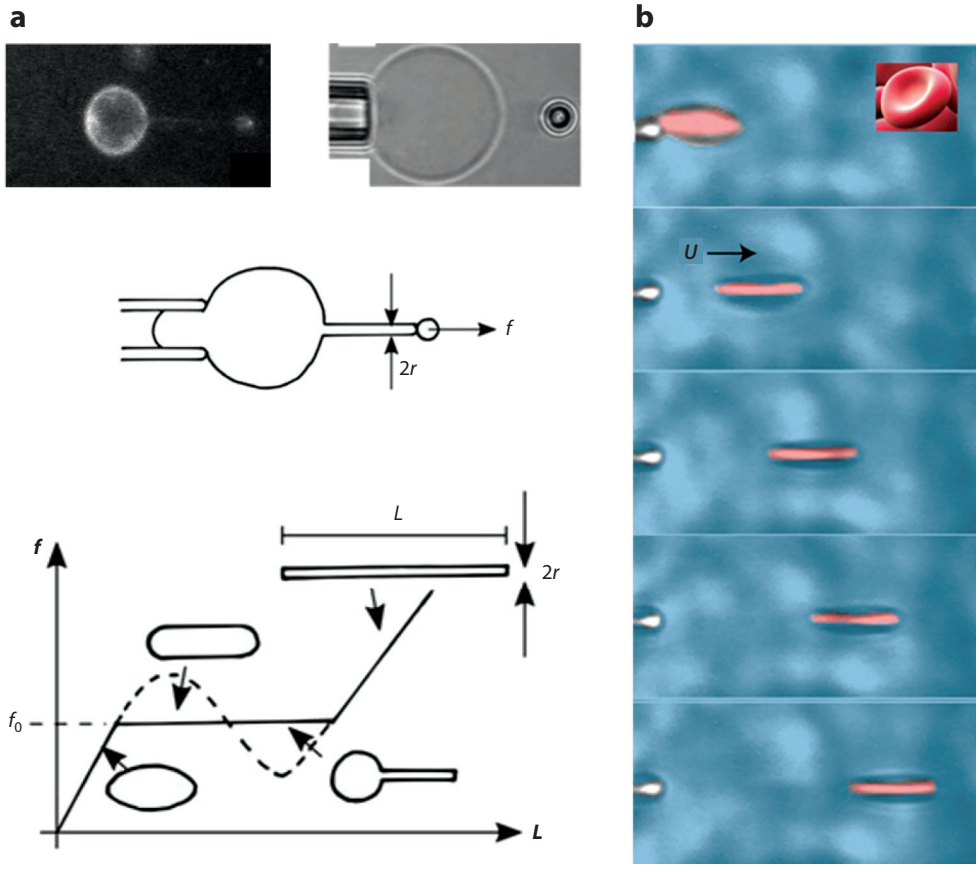

Figure 8

Extrusion of membrane tube from (*a*) vesicles and (*b*) red blood cells. Panel *a* adapted with permission from Reference 49. Copyright (2003), American Chemical Society. Panel *b* adapted with permission from Reference 50. Copyright EDP Sciences, 2003.

the nonlinear relation between the force and the velocity of extrusion by a thinning of the tube when the viscous stress increases (52). Manufacturing micro-structured substrates to attach dozens of cells, it is possible to establish statistical laws characterizing the extrusion of nanotubes of different cell lines, and to determine the effect of drugs or genetic mutations. The membrane nanotubes are used in vitro and in vivo to transport active molecules between vesicles or cells. We have shown that the transport is achieved by a Marangoni flow from the tense vesicle toward the soft vesicle (53).

5.1.4. Antagonist wetting: "fried eggs droplet." Rhône-Poulenc was interested in the wetting of mixtures in which the components have antagonist wetting properties. They came to me with a bottle filled with sticky complex liquids. I simplified the system, using a polymer in solution in a good solvent: the monomer. With R. Fondecave (54–56), we explored the laws of wetting of polymer solutions on model surfaces (salinized wafer) in an antagonistic situation: The solvent totally wets the surface, but the molten polymer wets it only partially (finite contact angle). By diluting the polymer, it was thought naively to encounter a wetting transition. In fact, we observed

a transition from a new type of leak-out in which the wetting solvent escapes from the drop and wets the substrate by forming an aureole around the drop, looking like a fried egg. Below this composition, the contact angle remains finite. A phase separation is coupled to the wetting.

5.1.5. Floating contact lines. The triple lines at liquid–liquid–air interfaces of a liquid puddle floating on an immiscible liquid are less studied than the contact lines of drops deposited on a solid substrate. They are free to move because they are not pinned to surface defects. X. Noblin studied the fluctuations of these triple lines, named triplons (57), studied in parallel at ENS using superfluid helium (58). We also explored the fast dewetting of liquid films on a liquid substrate and observed a cascade of shock waves (capillary waves in the front, gravity waves in the back) (59).

5.1.6. DNA under strong flow: trumpet and stem-flower. In labeling DNA with chromophores, Steven Chu of Stanford University was able to observe a single macromolecule and manipulate it with optical or magnetic tweezers: He visualized the reptation of one chain in a polymer solution. In parallel, I described the deformation regimes of a DNA molecule attached at one end and subjected to a uniform flow (velocity V) (60). I predicted for the configuration of the DNA a shape of a "trumpet" of size L (**Figure 9*a***), obeying simple scaling laws, and I sent my article to Chu. He told me, "Thanks to you, we did the experiments but your result is wrong!" I realized that the regime of the trumpet is valid only for a narrow range of velocities, and above a threshold velocity, we predicted a stem-and-flowers regime (**Figure 9*b***) (61). The total length L does not obey simple scaling laws, but the length of the flowers does.

With Buguin, we became interested in the unfolding and relaxation of the globular DNA in bad solvent. This work could yet have an impact on the denaturation of proteins. It also led to a new theoretical model of the collapse of a polymer chain suddenly placed in bad solvent. We then described the relaxation of a chain initially stretched, which reforms a coil from the free end, in collaboration with P. Cluzel and J.L. Viovy, who watched the relaxation of highly stretched DNA molecules. This model can also describe the helix-coil transition of synthetic polypeptides. With Pincus, I studied the transient regimes: the unfolding of the chain when, at time $t = 0$, a force or a flow is applied. I studied the eigen modes of flexible chains stretched by a flow in the shape of trumpets (62).

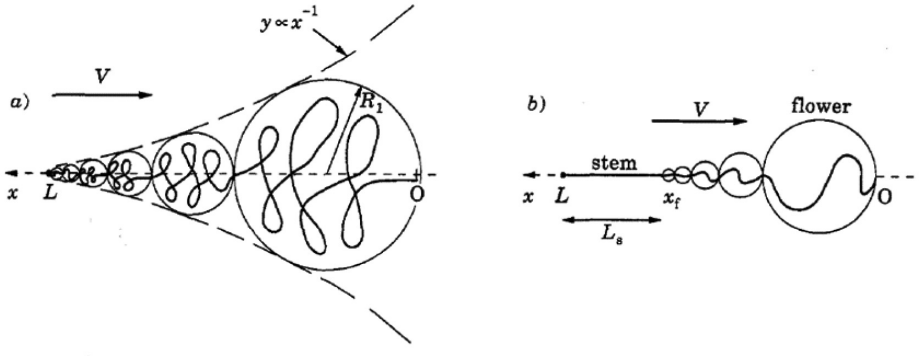

Figure 9

Deformation of a tethered chain under uniform flow: (*a*) trumpet and (*b*) stem and flower. Figure reproduced with permission from Reference 61. Copyright EDP Sciences, 1993.

5.1.7. Opening of transient pores. The nonspecific adhesion of giant and fluctuating vesicles to substrates was first studied by fluorescence microscopy by Olivier Sandre, who saw that strong adhesion can lead to the bursting of the vesicle. To slow down the dynamics, I told Olivier to use a viscous solvent, and a great discovery occurred! He saw the opening and the closure of a succession of transient pores. That was in June. Before summer vacation, it was published in the *PNAS* (63).

When a floppy vesicle (**Figure 10*a***) is stretched by an external action (**Figure 10*b***), pores open to relax the tension of the membrane (**Figure 10*c***). If the vesicle is immersed in a very viscous liquid, macroscopic pores open and close slowly because the leakage of the internal liquid is slowed down. In water, the leak is so fast that the pores close again before reaching an observable size. We performed a complete theoretical description of the dynamics of these transient pores.

The dynamics of the closure of the pores is ruled by the line energy associated with holes in the membrane. We have used transient pores as line tensiometers. Karatekin et al. **(**64) studied the role of surfactants on the mechanical properties of the membrane and the line energy. Some surfactants can drop this line energy by a factor of a hundred and make the membrane permeable. We tested several families of surfactants based on their hydrophilic/hydrophobic balance and their affinity for insertion into the membrane.

These large membrane permeabilities, induced by tension and favored by certain surfactants, may have applications in the transfer of drugs or to understand certain biological processes (endocytosis, exocytosis) (65). They are now a model for the pores observed in the nuclear membrane, when cells migrate in small capillaries or through the extracellular matrix. These permeabilities can also be harmful to the life of our cells.

Later, we extended these studies to the bursting of asymmetric light-sensitive polymersomes induced by curling (66) observed by E. Mabrouk and M. Li (**Figure 10*d***), which represents a new phenomenon because the light induces an increase of surface area of one of the two leaflets, which should lead to a decrease in membrane tension and not an increase that usually causes the bursting. I proposed a mechanism inspired by a very simple and beautiful experiment shown to me by E. Reyssat when visiting Lakshminarayanan Mahadevan at Harvard University: the curling of tracing paper gently deposited at the surface of water, caused by the swelling of one side of the paper (67). We suggested that the growth of a pore in polymersome membranes is driven by the same curling instability. The opening of the pore relaxes the curvature energy stored in the membrane as shown by the membrane curling of the rim (**Figure 10*d***).

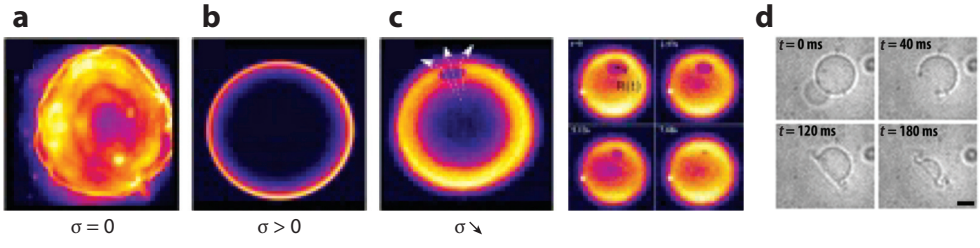

Figure 10

(*a*) Floppy vesicle. (*b*) Tense vesicle. (*c*) Opening and closure of transient pore. (*d*) Light sensitive polymersome bursting under UV illumination. Panels *a*, *b*, and *c* adapted with permission from Reference 63. Copyright (1999), National Academy of Sciences, U.S.A. Panel *d* adapted with permission from Reference 66. Copyright (2009), National Academy of Sciences, U.S.A.

5.2. Living Matter 2008–2018

Over the past ten years, our PCC laboratory has been moving toward cellular organization under the impetus of the new Department of Developmental Biology. Our culture in soft matter, critical phenomena, liquid crystals and self-organized liquids, and wetting brings new points of view to biologists. Thus, in the early stages of *Drosophila* development, a cellular organization close to a two-dimensional foam exhibits symmetry breaking with an isotropic → anisotropic organization that is similar to that of liquid crystals. A bold idea of Prost was the analogy between cancer and first-order phase transition, that is, discontinuity. A tumor would be indicative of growth instability and could only grow beyond a critical radius of nucleation; this was an idea that we tried to test and was the starting point for my work on cell aggregates, which has jostled the field.

We have introduced and worked on the broad field of entangled active matter, a novel class of nonequilibrium materials composed of many interacting units that individually consume energy and collectively generate motions or mechanical stresses. Unlike schools of fish and flocks of birds, both ants and cells can support static loads. This is because both cells and ants are also entangled, so that the individual units (cell or ant) are bound by transient links. With David Hu, we explored and established analogies between aggregates of both ants and cells (68).

For experimental purposes, assemblies of cells are among the simplest examples of active matter made of live entities. Increasingly, biologists, pharmacologists, and toxicologists are using cell aggregates as substitutes to animal studies. They are reliable and cost-effective systems for drug screening, bridging the gap between 2D cell-based assays and animal studies.

Our team, in collaboration with biologist Sylvie Dufour, has been working on applying soft matter physics (69) to study the biophysics of model tissues (tissue rheology, aspiration, spreading, mechanosensitivity, wetting and dewetting, and adhesion and fracture). Our studies of phase transitions in liquid crystals and instabilities of wetting films have been useful for understanding the spreading of cell aggregates and wetting transitions by playing on adhesion with substrate and intercellular adhesion. The results obtained from such analogies have suggested important implications for both tissue development and cancer. In September 2013, I was appointed Professor Emeritus, my group Surfaces Douces was dissolved, and I joined Joanny's theoretical group.

Since 2014, I have collaborated with Françoise Winnik's team in Japan on inert matter–living matter hybrid systems with two main questions: (*a*) Can nanoparticles stick cells together and substitute for cell adhesion molecules, and (*b*) can molecular noise give movement to the inert macroparticles active granular matter?

5.2.1. Cellular dewetting. We have previously described the dewetting of a liquid film by nucleation and growth of holes (**Figure 11*a***). A similar phenomenon had been observed with cells.

At the single-cell level, we studied the formation of holes in cells in collaboration with E. Lemichez (Nice). Pathogenic bacteria migrate from blood and lymphatic vessels to host tissues by opening transient macro apertures (MAs) in endothelium cells (70). To accomplish this, *Staphylococcus aureus* infect cells with EDIN (epidermal cell differentiation inhibitor), which produces a sudden disruption of the contractile cytoskeleton network. Cell membrane tension is no longer resisted by contractile acto-myosin fibers, leading to the opening of MAs, whereas cells infected with the inactive $EDIN_{R185E}$ remain intact (**Figure 11*b***). The opening is opposed by the line tension at the rim of the hole, which is induced by specific lipid sorting in the curved membrane. This induced line tension limits MA maximal size and eventually closes the hole, limiting endothelium permeability and preventing cell death. We modeled the opening and closure of MAs (71) by analogy with the dewetting of a liquid film (33) and transient pores in vesicles (63, 64). We

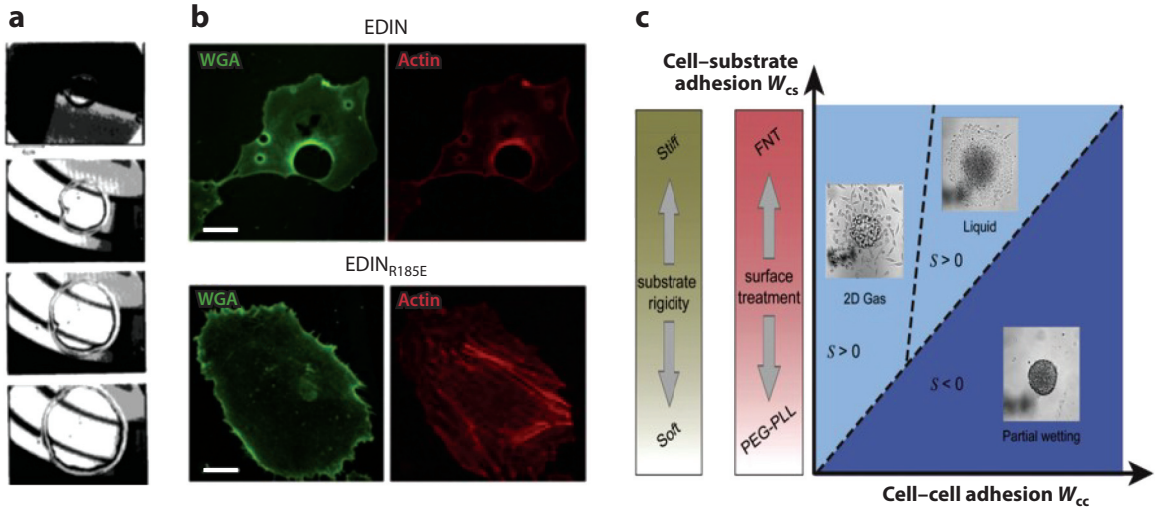

Figure 11

(*a*) Snapshots of the opening of a dry patch in a liquid film. (*b*) Opening of MAs and disruption of the actin cytoskeleton in endothelial cells intoxicated with EDIN, whereas cells infected with inactive EDIN$_{R185E}$ remain intact. The membrane is stained in green with WGA and the actin in red. Scale bars are 10 μm. (*c*) Wetting phase diagram of cellular aggregates. Abbreviations: EDIN, epidermal cell differentiation inhibitor; MA, macro aperture; WGA, wheat germ agglutinin. Panel *a* adapted with permission from Reference 33. Copyright (1991), American Physical Society. Panel *b* adapted from Reference 70. Copyright (2006), Rockefeller University Press. Panel *c* adapted with permission from Reference 69. Copyright (2012), The American Association for the Advancement of Science.

calculated the minimal radius for hole nucleation, as well as the maximal MA size as a function of the initial membrane tension, assuming a constant line tension T. We showed that the radius of a transient MA obeys simple scaling laws if T is small, leading to large MAs (71).

At the multicellular level, we have shown that cohesive cellular monolayers deposited on nonadhesive substrates are metastable and "dewet" by nucleation and growth of dry patches (72). The dewetting can be induced either chemically by a nonadhesive surface treatment or physically by a decrease in the substrate rigidity. We interpret the dynamics of growth of holes in the monolayer by an analogy with the dewetting of viscous films. This analogy can be used to estimate parameters characterizing the mechanical properties of cellular sheets.

5.2.2. Spreading of living drops. Since 2008, we have started a new research project on the characterization of the mechanical properties of biological tissues, the role of cell–cell adhesion on the tissue mechanics and eventually on the conditions for the growth of cancer tumors and formation of metastasis. Our studies are performed on spherical cellular aggregates, which are useful systems studying the mechanical properties of tissues because the adhesion energy between the cells can be controlled. We have used murine sarcoma (S180) cell lines transfected to express various levels of E-cadherin molecules at the surface of the cells in collaboration with Dufour, thereby controlling the intercellular adhesion energy, and CT26 murine carcinoma cells in collaboration with D. Vignevic, who is interested in the role of fibroblast in cancer extravasation.

We have studied the spreading of spheroidal aggregates of cells (S180), expressing a tunable level of cadherins (adhesion energy W_{cc}), on glass substrates decorated with fibronectin PEG mixtures (adhesion energy W_{cs}) (73). As shown in the phase diagram (**Figure 11*c***), we observed both partial and complete wetting depending upon the sign of the spreading parameter $S = W_{cs} - W_{cc}$. We monitored the contact area by optical interferometry and the profile by

side-view microscopy. At short times, the aggregate flattens, and the contact area increases as $t^{2/3}$. We interpret these results by modeling the aggregate as a viscoelastic droplet. At long times, we observe a precursor film with two possible states: in strongly cohesive aggregates this film is in liquid state, whereas in weakly cohesive aggregates the constitutive cells escape from the aggregate, forming a 2D gas. The progression of a noninvasive tumor into a metastatic malignant carcinoma, known as the epithelial-mesenchymal transition, can be interpreted as a wetting (liquid–gas) transition. On soft gels decorated with fibronectin and strongly cohesive aggregates, we observed a wetting transition induced by the substrate rigidity (74). We modeled the spreading dynamics of the monolayer expanding from the aggregate by balancing driving forces exerted by motile cells at the film periphery and viscous forces associated to the penetration of the cells from the (3D) aggregate into the (2D) film. By confocal microscopy, Grégory Beaune observed this new mechanism named permeation by tracking a single cell (75). Using particle imaging velocimetry, we characterized the flow field versus substrate rigidity. If cells spread like a viscous liquid on stiff substrate, the flows become irregular, with the formation of holes as the rigidity decreases. This work will shed light on the dynamics of tissue spreading occurring during cancer progression and embryonic development.

5.2.3. Aspiration of living drops. We have developed a new method based on a micropipette aspiration technique to measure the viscoelasticity and the surface tension (76) of cellular aggregates. As shown in **Figure 12**, the aspiration curve has two distinct regimes; a rapid deformation followed by a slow flow. This creep behavior is a signature of viscoelastic materials. At short timescales the material deforms like an elastic rubber, whereas at long timescales it flows like a liquid. Surface tension, viscosity, and elastic modulus of these aggregates have been deduced by analogy between cellular aggregates and viscoelastic liquids. We found that the surface tension of

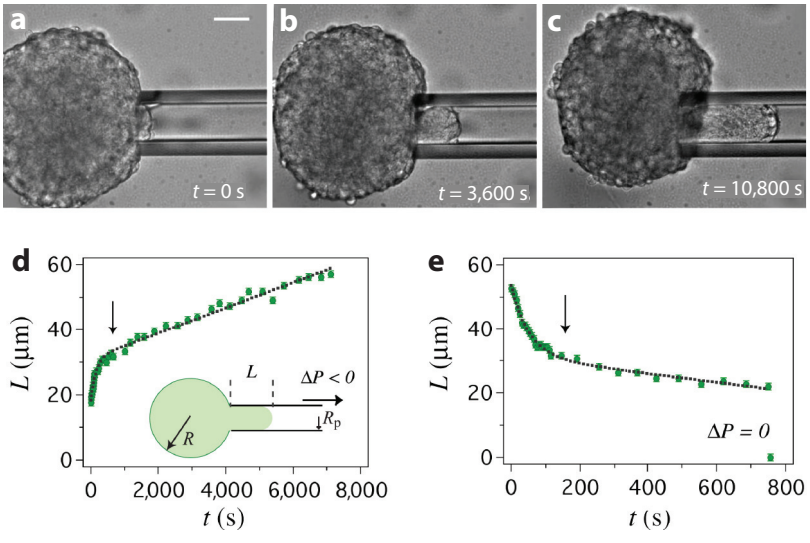

Figure 12

Micropipette aspiration of spherical cellular aggregates. (*a–c*) Snapshots of aspiration of an aggregate inside a pipette, scale bar 50 μm, $\Delta P = 1{,}400$ Pa. (*d*) Aspiration and (*e*) retraction cycles for an aggregate at $\Delta P = 1{,}200$ Pa. From $L(t)$ one can measure the surface tension, the elastic modulus, and the viscosity of the tissue. Figure adapted with permission from Reference 76. Copyright (2010), American Physical Society.

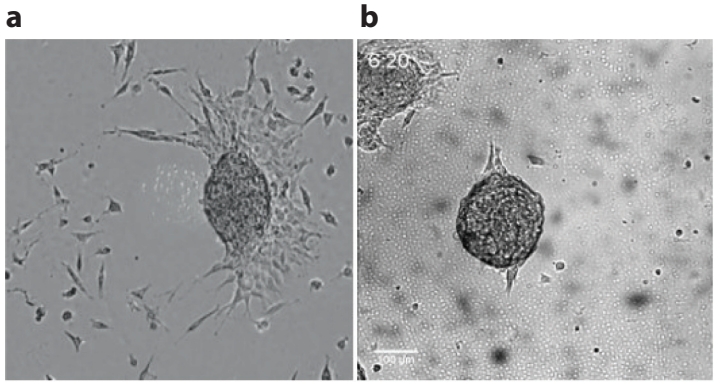

Figure 13

Cell aggregates on soft gels move spontaneously. They crawl with a stick-slip motion and adopt (*a*) the fan shape of giant keratocytes or (*b*) bipedal running spheroids. Figure reproduced from Reference 78.

the aggregate is stress dependent, suggesting that upon the application of an external stress, tissue cohesion is reinforced.

We observed that aggregates behave like viscoelastic pastes (76). However, Karine Guevorkian showed that, unlike an inert fluid, the aspiration leads to an aggregate's reinforcement, which for a narrow range of pressures, results in pulsed contractions or "shivering." We interpreted this reinforcement with David Gonzalez-Rodriguez as a mechanosensitive active response of the acto-myosin cortex (77).

5.2.4. Spontaneous migration: giant keratocytes. Single cell migration is studied extensively, but processes such as embryonic development or tumor metastasis often require the collective motion of a group of cells. We have observed a spontaneous collective migration of cellular aggregates on soft gels coated with fibronectin. During the spreading, the cell monolayer expanding outward becomes unstable and dewets (78). This leads to symmetry breaking of cell polarities, causing the entire aggregate to move. Decreasing the substrate rigidity, we observed stick-slip motions and different shapes (**Figure 13**): giant keratocytes, where the lamellipodium is a multicellular monolayer expanding in the front and retracting in the back, and bipedal "running spheroids" on ultrasoft substrates. We characterized the flow field and the stresses that drive the migration. Our study provides a powerful in vitro model of the mechanisms of multicellular cell migration and cancer invasion.

5.3. Cellular Aggregate-Nanoparticles Hybrid Systems

In January 2015, I received with Winnik a fellowship from WPI International Center for Material Nanoarchitectonics (MANA-NIMS) for "Developing new theories based on soft matter physics to describe and understand the mechanical properties of cells as they interact with nanoparticules." Grégory Beaune, my postdoc in Institut Curie, accepted to move to Japan.

We have studied how cells and particles play together. We named this project "eating-dancing": On the one hand, nanoparticles and microparticles are eaten by the cells or adsorbed on the cell's membrane. On the other hand, macroparticles, which are too big to be digested, are put into motion by the cells, and they dance: This is our project for the next few years.

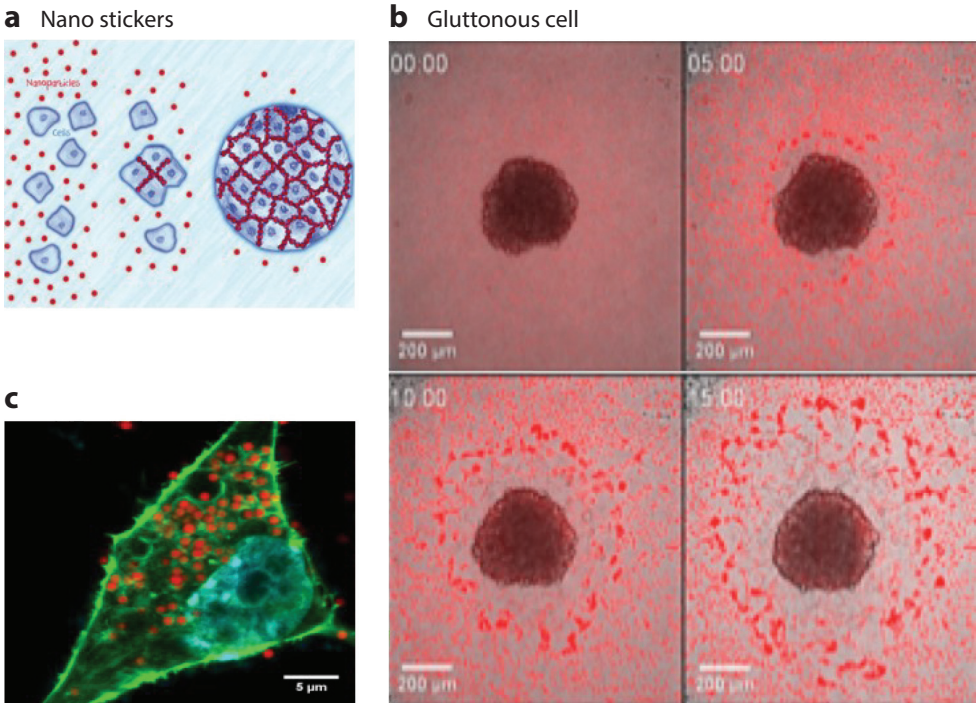

Figure 14

(*a*) Nanoparticles sticking cells together. (*b*) Multicellular uptake of MPs. Spreading of a cell aggregate on glass decorated with fluorescent PsCarbo1000 MPs with surface fraction of 0.23, observed in bright field at $t = 0$, 5, 10, and 15 hours. (*c*) Confocal microscopy of a cell at the periphery of the film spreading on MPs (*shown on the right in panel b*); the particles occupy a large fraction of the cell's volume. The cytoskeleton is stained in green, the nucleus is stained in blue, and the fluorescence of the beads is red. Abbreviation: MP, microparticle. Panel *a* adapted from Reference 79 with permission from the Centre National de la Recherche Scientifique (CNRS). Panels *b* and *c* adapted from Reference 80. Copyright (2017), The Royal Society of Chemistry.

5.3.1. Nano stickers. We show that nanoparticles (20 nm in size) can be used as a glue, nano stickers, to enable the formation of self-assembled aggregates by promoting cell–cell interactions (79) (**Figure 14*a***). We find that carboxylated polystyrene nanoparticles are more efficient than the silica nanoparticles of the same size, which were reported by Leibler to induce fast wound healing and glue soft tissue. Nano stickers, by increasing the cohesion of tissues and tumors, may have important applications for tissue engineering and cancer treatment.

5.3.2. Microparticles: gluttonous cells. We study the spreading of cell aggregates deposited on adhesive substrates decorated with microparticles (1 micron in size). A cell monolayer expands around the aggregate. The cells on the periphery uptake the microparticles by phagocytosis, clearing the substrate and forming an aureole of cells full of particles (**Figure 14*b*,*c***). We study the dynamics of spreading, the width of the aureole, and the level of cell internalization. This leads to an easy, fast, and inexpensive cell–particle internalization measurement (80). We want to study the role of the rigidity on phagocytosis by using microfluidic fabrication of soft jelly beads.

5.3.3. Project: hybrid dead–living matter. After Japan, I continue to collaborate with Beaune who joined the Active Matter Group of J. Timonen in Finland. Our aim is to study granular active matter by using hybrid aggregates of microparticles and cells. The hybrid aggregates will be prepared by flocculation of a solution of micrometric passive beads (soft or rigid) and active cells. For micrometric particles, we do not expect Brownian motion: Aggregates of beads are frozen. However, the aggregates of cells are liquids because the activity of the cells produces a large nonthermal noise: they form spheroids to minimize their surface energy. Our project is to investigate the conformation and the physical state of cell-particle hybrid aggregates versus the particle volume fraction, for which we predict jamming transitions and phase separations. These fundamental studies on the mixture of dead and living matter will have applications for other types of mixtures of active matter at various scale lengths, such as, for example, cell mixtures or a cell's nucleus. As in the case of the genome of eukaryotes that is partitioned into domains of functionally distinct chromatin states, euchromatin-containing active genes and heterochromatin-containing silent genes, we anticipate that hybrid aggregates will contain domains enriched/depleted in particles. Phase separation is also predicted by simulations and analytically predicted in a mixture of particles with different levels of activity in which one phase is enriched in active particles (cells) and the other in passive particles.

My soft matter garden has been published in articles and a few books (**Figure 15**).

Figure 15

Books coauthored by Françoise Brochard-Wyart.

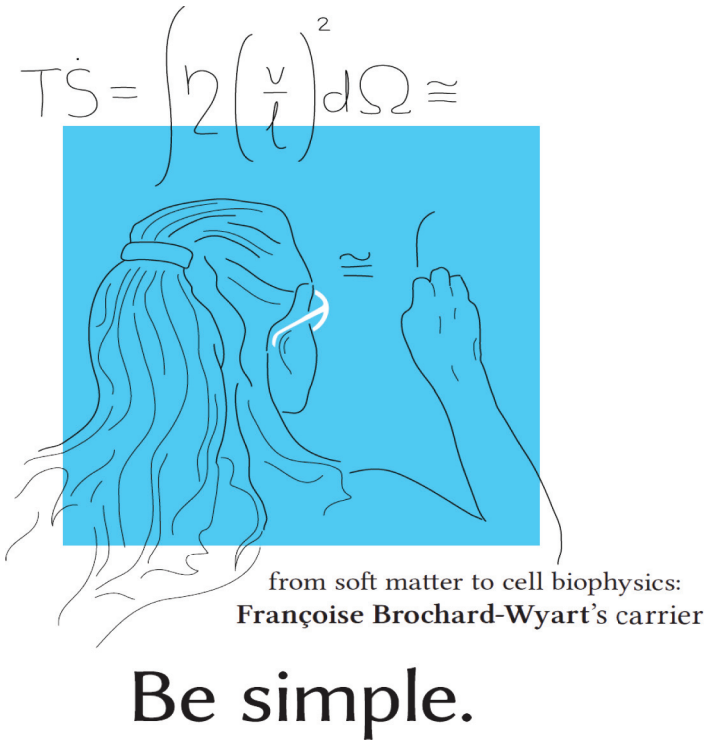

Figure 16

Poster for a meeting on Oct. 1–3, 2018, to celebrate the scientific career of Françoise Brochard-Wyart and her contributions to soft and biological matter. Drawing by Basil Gurchenkov.

In my career, I remain a concrete theoretician, working closely with experiments and in collaboration with biologists who present us with complex situations in which we must unmask a simple idea and develop it. Gonzalez-Rodriguez offered to me a cup that had "Be simple" written on it. This is the name of the meeting held in October 2018 to celebrate my scientific career (**Figure 16**).

Finally, I will quote the conclusion of Yves Quéré's speech, which expresses my style of work and the meaning of my life.

> The 'hallmark' of your scientific output is very strong: most of your articles are those of a theoretician (you) who is joined by excellent experimentalists, in small groups that you form, inspire and animate. You're not the only one working in this way but you do it in an exemplary way. You, dear Françoise, gave birth to a lot of new knowledge, but also to many beings, the hundreds of your university students, the dozens of researchers with whom you worked who all love you, and also of course to six wonderful children whom I am glad they are all present today at your side.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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I thank all my colleagues and collaborators in France and abroad for their friendship; my students and my postdocs who achieved all these beautiful experiments; Gregory Beaune and Françoise Winnik for their wonderful collaboration at the Mana Institute in Tsukuba; Basil Gurchenkov for his drawing "Be simple"; Claire Wyart, Madeleine Veyssié, Thomas Risler, Uzay Girit, David Gonzalez-Rodriguez, and Nada Khalifat for their precious advice in the production of this text; and last but not least Gisèle Vergand who took care of my children like a second mother when I was working and traveling.

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