Patterns and regularities in the aggregation of living organisms

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Abstract

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To many readers this paper will appear somewhat unconventional. There is a simple reason for that. It results from a collaboration between physicists and entomologists. Physicists always try to discover fairly general rules. Of course, all rules and laws have limitations, but the broader the better[1]. This is why this paper does not limit itself to just one specific species but rather offers a comparative approach involving several species. This comparative perspective is one of the unconventional features we were referring to.

A second characteristic of this paper can be explained as follows. Physics experiments are more than just careful observations; they always ask Nature specific questions. If an experiment is well designed[2] Nature will provide a clear answer. The present study was set up in a similar way. The question that we submit to Nature is the following.

Aggregation phenomena are observed in many living organisms from myxobacteria to humans. Can we get new insight by analyzing them from a comparative perspective?

The graph in Fig. 1 provides a broad view of binding energies in various systems. The binding energy is one of the two factors which conditions clustering phenomena, the other being the agitation pressure (as will be explained in more detail shortly). As a result of these binding energies there is a release of energy during an aggregation process. This energy release is well documented for nuclei, atoms and molecules. For the gravitational case it is not immediately obvious that when one brings together two masses initially several meters apart, they will become warmer. As a matter of fact this temperature increase is very small (of the order of 10^{-15} degree) and completely undetectable. For this effect to become more massive one must observe it on a much larger scale for instance during the process which leads to the formation of a star. In this case the energy from the gravitational aggregation provides enough energy to heat the hydrogen of the protostar to the ignition point of hydrogen fusion, some 15 million degree Kelvin.

Is there also a release of energy for the clustering of myxobacteria or bees? In the first case, according to the regression line, it would be about one million times smaller than for molecules that is to say of the order of 10^{-6} degree, still too small to be detectable[3]For bees or desert locust the temperature increase would be even much

[1] As an illustration one can recall that the law of free fall discovered by Galileo four centuries ago applies to balls of metal as well as to apples, nuts or hailstones and many other objects falling in air. Yet, it does *not* apply to falls occurring in water instead of air.

[2] Which in particular means that by choosing appropriate experimental conditions the ratio signal/noise should be made as high as possible.

[3] It is true that bacteria can produce a substantial amount of heat in some circumstances, for instance during the decomposition process of organic matter, but in this case the heat is produced by their activity not by any clustering process.

smaller. It is true that the aggregation of desert locusts give rise to swarms of several billion insects but the density of such swarms is too small to make this effect detectable.

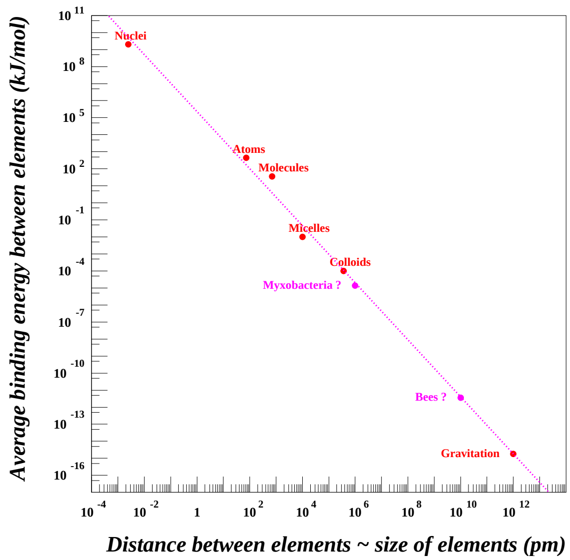

Fig. 1 Binding energy as a function of size. The distances on the horizontal scale are given in picometer (1pm=10^{-12} m), the energies on the vertical axis are given in 1000 joules per mole. The 5 points for physical systems are in red. They display three different forces: nuclear, electrostatic (for atoms, molecules, micelles) and gravitational forces. As is well known, the orders of magnitude of the strength of these forces are widely different. Micelles are aggregates of long molecules (of a molecular weight of several hundreds) which on one end have an O-H part (or similar) that is attracted toward water molecules. The heat release (or absorption depending upon conditions) for micelles is documented in Garidel et al. (2005). The colloid figures refer to an experiment involving polystyrene latex balls of an average diameter of 360 nm. (Jódar-Reyes et al. 2001). The points for living organisms are in magenta. An interrogation mark has been added because the binding energy of such systems have not been measured yet. The equation of the regression line is: $\ln E = a \ln d + b, \quad a = -1.7 \pm 0.09,\ b = 12 \pm 1$; the error bars refer to a confidence level of 0.95. *Source: The data for the nuclei are for a reaction involving the fusion of lithium and deuterium nuclei. The data for atoms and molecules follow standard orders of magnitude of the binding energy for a molecule of water and for the hydrogen bond between different water molecules. The gravitation point corresponds to two masses of 1 kg whose distance is reduced from infinity to a distance of 1 meter (for the sake of simplicity). It can be noted that for objects of macroscopic size (starting with the latex ball colloids) the notion of mole has no longer any meaning. The data for colloids and micelles are from Jódar-Reyes et al. (2001) and Garidel et al. (2005) respectively.*

Significance and role of aggregation processes

The paper's title mentions "aggregation of living organisms". In line with this title the experiments described in the second part of the paper will be restricted to the study of aggregation in insect populations. However, one should keep in mind that many crucial steps in the evolution of the universe relied on aggregation processes.

Here are a few illustrations[4].

- The core regions of stars were able to develop high temperatures (in the range of several million degrees) through the energy released by the process of gravitational aggregation. In this way they became the factories of most elements present in the universe.
- Aggregation in specific species of bacteria resulted in some of the earliest instances of cellular differentiation. Examples will be given below.
- Many landmark steps in the evolution of mankind such as storing grains, developing written languages, creating religious and political forms of social organization, were made both necessary and possible because of the aggregation of people in towns and cities.
- Many cultural revolutions or scientific breakthroughs occurred inside networks of closely connected people. As a matter of fact, the interactions may have been essential in creating favorable conditions for this kind of synergy. As illustrations, one can think of the start of the Renaissance in the Italy of the *Quattrocento* (a word that is a contraction of *millequattrocento* which means 1400), the impressionist revolution in late 19th century France, the revolution of quantum mechanics at the university of Göttingen in Germany around 1925 or the Internet Revolution in California in the last decades of the 20th century.

Needless to say, in this paper we wish to go beyond such fairly loose qualitative statements. Nevertheless, it is certainly important to keep in mind the broad significance of aggregation processes.

Because no real framework is so far a The approach used in this paper will be to use what we know about physical systems as a guide or a beacon in order to find our way in trying to understand systems of living organisms. In other words, physical concepts and notions should be seen as tentative working assumptions. Of course, it is our hope that they can help us to define a conceptual framework for living systems, but those that are found unsuitable will just be dropped.

Aggregation seen as a competition between two effects

Which clustering

There are several kinds of clustering which may rely on completely different mechanisms. Therefore it is of cardinal importance to define as clearly as possible the kind of clustering in which we are interested.

Broadly speaking, one can distinguish 4 kinds of circumstances leading to cluster-

[4] More details about three of them can be found in Roehner (2007 in the beginning of chapter 1).

ing.

(1) Clustering may occur because the individuals are attracted to the same place by an exogenous factor. For instance, vultures may cluster around the carcass of a dead animal or dolphins may be attracted by a big shoal of fishes.
We will call this kind of clustering "bait induced clustering (BI-clustering)". In this expression, the term "bait" has a broad understanding. Apart from food, it may also include light (or darkness), humidity, a source of heat, and so on.

(2) Clustering may occur because many individuals do the same thing at the same moment. An example is provided by the nuptial flight of ants or bees. Different colonies of the same species use meteorological cues (for instance, no rain, little wind) to synchronize the release of males and queens so that they can mate with individuals from other nests, thus avoiding inbreeding. Another example is provided by the seasonal mass migration of impalas, antelops or gnus toward other feeding places.
A similar kind of clustering would be the gathering of many people for a protest demonstration. The individuals cluster because their actions are synchronised. Clustering that occurs for the purpose of wintering among lady beetles or other beetles can be seen as belonging to the same class. Clustering induced by starvation as observed in myxobacteria (e.g. see Kuner and Kaiser 1982[5]) can also be put into this class.
We will call this kind of clustering "clock induced clustering (CI-clustering)".

(3) A beehive, a nest of ants or a city can be seen as a form of clustering in the sense that these places have population densities that are much higher than the average density. In contrast with the two previous forms of clustering which were short-term phenomena lasting less than one day, these clusters have a duration of several years.
We will call that clusterings "nest clustering (N-clustering)".

(4) Finally, there is the clustering that will be observed in our experiments which will be set up in a way that excludes all exogenous factors. This means that one tries to avoid any gradient of light, humidity, temperature, and so on. However, it is not sufficient to take into account such obvious factors. For instance, it turns out that ants (and also bees to some extent) preferentially gather in the corners or on the edges of their container. In other words, designing the container and the experimental protocol already requires some understanding of the phenomenon. When we started our experiments we relied heavily on the pioneering work of Jacques Lecomte (1949,

[5]In fact in this experiment starvation alone was not sufficient for triggering the aggregation process. An appropriate concentration of calcium chloride was also required. The degree of aggregation was controled by the concentration of calcium chloride: For a concentration under 0.1 millimole/liter there was no aggregation; between 0.1 and 1 the process lead to patches of bacteria, above 1 it lead to a tight aggregate that involved the entire population.

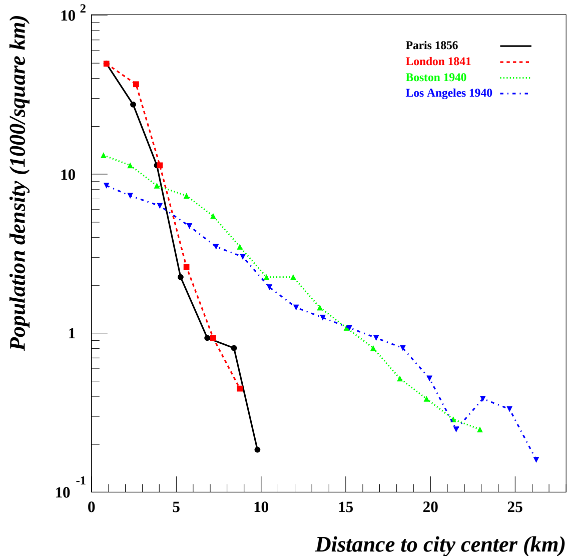

Fig. 1 Population density in cities from center to outskirts. In cities the population density $d(r)$ decreases exponentially from the city center to the periphery: $d(r) = A\exp(-r/q)$, where r is the distance to city center. For the 4 cases shown in the graph the characteristic length q took the following values (in km): Paris: 1.7, London: 1.1, Boston: 5.3, Los Angeles:6.4. The availability of means of mass transportation appears to be a key-factor for q. One must also take into account the fact that it takes decades for a city to move from one density pattern to another. For Paris in 1931, q was still not higher than 2.1 despite a significant development of surface and underground means of public transportation. In conclusion, it does not seem that we can learn anything significant about inter-individual interactions from the characteristics of population density patterns. *Sources: The data are adapted from Clark (1951). For Paris Clark relied on Meuriot (1898); for London, Boston and Los Angeles he used Census data.*

1950, 1956).
This form of clustering will be called "basic clustering (B-clustering)".

Why do we call the 4th type *basic* clustering? It is basic in two ways. (i) Because exogenous stimuli are discarded, it is a simpler form of clustering than what can be observed in the field. (ii) The other three forms of clustering rely on the communication mechanisms that are at work in basic clustering. This is fairly obvious for nest-clustering and for swarming. For bait-induced-clustering it is less obvious because one can imagine individuals to be separately attracted toward the bait. However, it is well known that in bees and ants food collection is a cooperative effect which involves the discovery of the bait followed by a recruitment process which brings more foragers to this place.

Competition between two forces in physical systems

In its essence, aggregation in physical systems is fairly simple. It is a competition between two effects:

- An attraction which tends to bring individual elements together.
- An agitation effect which tends to make each indidual follow its own peculiar

trajectory.

Aggregation occurs when the attraction dominates, dislocation occurs when the agitation forces dominate. This makes aggregation phenomena a source of information about attraction forces. For instance, the melting point of solids or the boiling points of liquids are good indicators of the strength of corresponding attraction forces.

Can one give a more precise definition of these two effects at least for physical systems? The attraction is due to attraction forces: short range nuclear forces in nuclei, van der Waals forces (which are due to electrostatic effects) between molecules, long range gravitational forces.

At first sight, the agitation effect may seem fairly clear too in the sense that would attribute it to the thermal agitation which, according to the kinetic theory of gases, is closely related with the kinetic energy of the molecules. Yet, in what sense can this agitation be defined as a force? As a case in point let us consider one of the huge interstellar clouds of particles that astrophysicists have discovered. Let assume that it is in equilibrium in the sense that it neither expands nor collapses. Because of gravitational attraction any random density spike around a point C would trigger an instability by attracting more particles toward C unless the attraction is counterbalanced by another force. This opposing force is the kinetic pressure[6] defined as $p_k = \rho < v^2 > /2$ where $< . >$ denotes an average over many particles. Is this force able to counterbalance the gravitational attraction? If in a volume V of radius r around C the density becomes $\rho' = \bar{\rho} + \Delta\rho$ the particles on the surface of V will indeed experience a net *inward* force equal to $\Delta f = 4\pi r^2 \Delta\rho < v^2 >$.

Are there also two competing forces in the clustering of living organisms?

The first two forms of clustering described above can be explained without any attraction between individuals. For nest clustering this is somewhat less clear. It is true that one can argue that people stay in towns and cities because of greater job opportunities but these jobs probably exist only because the level of interaction is higher in cities than in the countryside.

How can one check wether there are indeed two opposite forces for basic clustering? As the experiment was set up in a way that eliminates other factors, the aggregation process can only be explained by inter-individual attraction. At the same time there must also be an agitation effect for otherwise clustering would occur invariably, irrespective of initial density or global number whereas observation suggests that number and density must obey specific conditions.

Can one give some indications about the nature of the attraction and agitation forces?

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[6] This pressure was introduced by Daniel Bernoulli (1700-1782) in the fairly different context of hydrodynamics in which there is no real need for the averaging notation $< . >$.

Several mechanisms can contribute simultaneously to the attraction effect: one can mention chemical pheromonon signals, visual signals, sound signals or touch signals through antenna contact.

The nature of the agitation effect is less obvious. In the previous subsection we introduved the notion of kinetic pressure. From the perspective of living organisms it has a great advantage over the more standard definition of pressure which relies on the shocks of the particles against the wall of the container for, obviously in contrast to particles, living organisms do not hit the walls. The two factors ρ and $< v^2 >$ which appear in the definition of p_k can both be measured just by observing the positions and motions of the living organisms over a short time interval. If a cluster is in a stationary state there must be an equilibrium between the attraction and agitation forces. The way the density changes from the center of the cluster to its periphery will give useful information about these two forces.

Evidence for the existence of dispersion forces

The effect of dispersion forces in a population of insects can be identifies through the following simple experiment.

One takes a test tube containing some 50 drosophila and one brings them all to the bottom of the tube by hitting a table with the bottom of the tube. Then, very quickly[7] one puts the tube on the table in horizontal position. Let us assume that the bottom of the tube is on the left. After a few seconds, some 5 flies will have reached the right-hand side, and may be 10 others will be in the middle of the tube. If one waits 5mn, the flies will be distributed fairly uniformly throughout the tube.

If one repeats the same experiment with "Tenebrio molitor" beetles one sees that after 5mn almost all insects are still together on the left-hand side of the tube.

We will see below how this experiment can be repeated to give more precise quantitative measurements.

Aggregation phenomena

In order to observe an aggregation effect the initial balance between attraction and agitation must shift in favor of the former. If one of the factors is much stronger than the other there will be aggregation or disaggregation effect. Thus, we never see any aggregation-disaggregation effect in solids because in this case attraction is much stronger than agitation which means that the system remains in a aggregated state. Similarly, we will not see aggregation effects among the cells of a living organism because they are held together by strong cohesion forces. In that case, as for solids, we are not even aware of the existence of agitation forces.

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[7]This movement must be fast because drosophila have a natural tendency to go upward.

At the other end of the spectrum we will not see any aggregation effect in a hot gas because in this case agitation is the dominant factor.Similarly, there are many species for which one does never see any aggregation effect. the obvious conclusion is that in such cases the inter-individual attraction is inexistent or at least very weak.

In other words, the main thing that the observation of an aggregation effect tells us is that in the system under consideration both attraction and agitation exist and that they are nearly of same strength. This is what makes aggregation phenomena of interest. Through them we can get information about attraction and agitation forces.

Depending on the system that we consider, the forces and factors which produce the attraction and agitation may differ but neverthless the previous mechanism must apply. Thus, our task is to identify (and possibly measure) the attraction and agitation factors.

This pressure is of crucial importance in the interstellar medium (mostly composed of hydrogen molecules) because it prevents gravitational collapse by counterbalancing gravitational attraction. It is only when the density reaches a critical threshold (of the order of 100 particles per cubic centimeter) that gravitational collapse will take place and lead to the formation of a new star In fact, density is not the only variable in this process. Temperature is quite as important. The theory proposed by James Jean suggests that the greater the mass of the cloud, the smaller its size, and the colder its temperature, the less stable it will be against gravitational collapse[8].

Thermal agitation exists as soon as the temperature of the system is higher than zero degree Kelvin. In solids one knows that this agitation consists in tiny vibrations of the molecules (or atoms) around their central positions but one cannot see any macroscopic effect of such vibrations. It is only through the occurrence of phase transitions that one can observe the effect of the competition between attraction and agitation. That is what makes the clustering effect important. It gives us an insight into the forces which hold the system together and into the agitation which brings about disaggregation.

With ever increasing temperature, any physical system will eventually reach the state of a hot gas in which agitation completely dominates attraction.

Role played by the number of elements in the cluster

For the sake of simplicity let us assume that the attraction force between individual

[8]More precisely gravitational collapse will occur when $kTr/GM\mu < 1$. k is the Boltzmann constant, T the absolute temperature, r the radius of the cloud, G the gravitational constant, M the total mass of the cloud and μ the mass of a particle i.e. approximately the mass of a hydrogen atom. Just as an illustration, if one takes $T = 1$ and for M the mass of the Sun the critical radius is found equal to 3,400 times the radius of the solar system up to Neptune. In other words, the cloud which gave rise to the Sun was much larger than the solar system. It is true that the assumption $T = 1$ was somewhat arbitrary but even with a temperature as high as $T = 10$ the critical radius would still be 340 times larger than the solar system.

elements (whether physical or living entities) is independent of distance. If the group contains n elements, any one of them will experience n two-body interactions f_2 , $n(n-1)/2$ three-body interactions f_3, $n(n-1)(n-2)/3!$ four-body interactions f_4 and so on. Altogether the binding force experienced by each element will be:

$$f_b = f_2 + f_3 + f_4 + \ldots$$

The previous argument does not hold for elements which are near the surface of the cluster. For such elements, the attraction forces will be divided by a factor $k > 1$; the precise value of k will depend upon the geometry of the boundary surface of the system. For instance, if the system is a "big" sphere k will be almost equal to 2 if locally the boundary can be approximated by a plane.

The previous arguments suggests the following predictions.

(1) As obviously all these forces increase with n one would expect that under a given threshold $n < n_c$ the attraction will be too weak to overcome the agitation factor.

(2) For clusters formed by groups which include more than n_c elements one would expect the average binding force per element f_b to increase with n. As n becomes larger two effects will play a rile simultaneously.
(i) First the proportion of elements located near the boundary will decrease because the number of bulk elements increases as r^3 whereas the number of boundary elements increase as r^2; thus the *proportion* of boundary elements will *decrease* as $1/r$.
(ii) Secondly, if the binding force has a limited range, a bulk element will interact with only a fraction $f\ n$ ($f < 1$) of the total number of elements.
The shape of the function $f_b(n)$ will give information about these effects.

Questions

Many questions immediately come to mind when we think about the phenomenon of aggregation. At the conceptual level it is convenient to make a clear distinction between equilibrium (that is to say concerning stationary states) properties and non-equilibrium (that is to say time dependent) properties although at the experimental level the two kinds of effects may overlap.

Equilibrium properties

One can mention the following questions.

(1) For physical systems it is the condensation curve $p = f(T)$ which represents the borderline between the two domains mentioned above: (i) the liquid state domain that is dominated by attraction (i) the gas state domain that is dominated by agitation. This suggests the following question: is it possible to identify (qualitatively and quantitatively) a condensation curve for systems of living organisms?

(2) For groups of insects it has been shown (see below the experiments performed by Lecomte (1949, 1950, 1956) that aggregation requires a minimum number of individuals. For *mellifera* bees this number is of the order of 70. This leads in a natural way to the question of whether there are similar effects in physical systems or in populations of bacteria.

In the field of nuclear physics these issues more specifically lead to the following questions. (i) Is there a "condensation curve" for atomic nuclei (ii) Does aggregation require a a critical number n_c of nucleons?

The answer to the first question is that the "condensation curve" is the line which separates stable isotopes from unstable isotopes. In nuclear physics textbooks this curve is usually defined in a coordinate system whose axis refer to the values of the numbers of protons (Z) and neutrons (N) but this does not give as clear an insight as the $p = f(T)$ curve. Indeed, whereas the pressure p is closely connected with intermolecular distance and thus with interaction strength, the binding energy of a nucleon depends upon the values of Z and N is a fairly complicated way. In the same way, whereas the temperature T is directly connected with molecular agitation, in nuclei there are various disrupting factors. For instance, the Pauli exclusion principle which does not allow two particles to have the same quantum numbers is a source of instability which forbids the (stable) existence of a nucleus composed of just two protons.
The second question about a possible threshold n_c has a simple answer which is "no" at least if one forgets the difference between protons and neutrons. Qualitatively, the fact that even small nuclei are stable is due to the high strength of nuclear forces at short range.

What else can one learn from observations made in the field of nuclear physics? Leaving aside the surface effect, it is observed that the binding energy per nucleon increases as n (rather than n^2 or n^3). In accordance with our previous argument this implies that the nuclear forces have a short range which includes only nearest neighbors, a conclusion that is confirmed by independent evidence.

Can one answer these same questions for systems of colloids? In this case the attraction strength can be controlled through the addition of what is called a coagulant. The mechanism can be explained as follows.

Most particles dispersed in water have a negative charge, so they repel each other, at least at short range. As a result, they form stable dispersions. Particles with a diameter of less than one micrometer will remain in equilibrium in midwater due to molecular shocks (which are also responsable of the phenomenon of brownian motion). However, when a positively charged *coagulant* is added, the particles become

neutral and then can attract each other through (weak) van der Waals forces. The big particles that they form are called flocs and because of their size they do not remain in equilibrium but, depending on their density, drift to the surface or fall to the botton. In other words, the analog of the condensation curve would be a curve $c = g(T)$ relating the concentration of the coagulant to the temperature for a given concentration of colloids. In experiments with colloidal suspensions one uses the notion of so-called Zeta potential in order to estimate the negative charges held by colloidal particles.
What should be done in order to answer these same questions for population of bacteria? One should observe whether clustering occurs or nor in experiments where the density of the bacteria would be changed. This is much easier to do for bacteria which are

The rationale for comparative investigations

To our best knowledge, in the past decades there have been few investigations focusing on this question from a broad comparative perspective.

In contrast there have been many studies and publications focusing on the detailed mechanisms of specific cases. For instance the aggregation of myxobacteria, unicellular micro-organisms without nuclei, and of *Dictyostelium discoideum*,an unicellular amoebae with a nuclei have been studied in detail in numerous papers.

To know the factors which are involved in such specific cases is certainly of interest. Yet, an obvious objection comes to mind immediately which can be summarized in the following argument.
For human affairs we enjoy the peculiar status of being both actors and observers. This dual role *ipso facto* gives us access to detailed knowledge about human actions. There can be no doubt that thanks to numerous historical accounts we have a detailed knowledge of the American, French and Chinese Revolutions or of major wars such as the American Civil War and the two World Wars of the 20th century [9]

Yet, does all this knowledge give us a real understanding of wars and revolutions? A good test is to ask whether or not we are able to make reliable predictions. The answer is left to the reader. From this argument one can draw two different conclusions.

The first one would be to say that the social sciences were unsucessful because human freedom makes all predictions impossible. The second conclusion would attribute this failing to the fact that, except for few and rare exceptions the social sci-

[9] Why did we add the precision "of the 20th century"? One should recall that there have been world wars before the 20th century. For instance, the Seven Years War (1754-1763) extended to all continents and the same is true for the successive conflicts between Britain (with its allies) and France (with its allies) that followed the French Revolution of 1789.

ences did not wish to adopt the comparative perspective that gave so excellent results in physics, chemistry and astronomy. When this approach is used it quickly appears that, human freedom notwithstanding, it is indeed possible to find patterns and rules.

In the wake of the triumph of physics, the comparative approach was much in favor in the second half of the 19th century and lead to major accomplishments in the social sciences. For instance, one can mention the discovery of some of the laws governing suicide by Emile Durkheim. Nowadays, for several reasons one of which is the current hyper-segmentation of social science research, the comparative approach has been largely put aside.

Of course, we do not wish to say that case-studies are useless, but rather that in order to get real significance they must be seen in a broader perpective through which they will become connected to one another.
The paper is organized as follows.
Finally, in the conclusion, we summarize our results and we discuss a possible agenda for further investigations.
For this review of aggregation phenomena let us start from what we know best, namely aggregation in physical systems. From there we will move to aggregation cases in populations of bacteria or , some of

Aggregation in physics

Rationale

Why do we start with physical systems? Thanks to the collective work of generations of physicists going back to the 16th century physics has the great advantage of being the most successful science. In addition, and contrary to a common opinion, there is no sharp separation between physical phenomena and those involving living organisms. Even life and death have their counterpart in physical systems. For instance, even under ideal conditions rechargeable batteries have a limited lifetime that can be measured in loadcycles[10]. Many other physical or chemical systems have a limited lifetime. (e.g. light bulb or even a simple metal wires that is bent repeatedly).

Physical aggregation phenomena

Regarding aggregation effects, three kinds of physical phenomena come to mind (i) condensation of molecules of molecules of vapor into liquid droplets (ii) liquid to solid transitions (iii) the aggregation process that may occur in an unstable colloidal system and lead to floculation or coagulation. A common characteristic of these

[10]The maximum number of load-cycles of a lead-acid battery used in cars is around 600 which when converted in years gives an average life expectancy of about 5 years. In contrast a nickel-cadmium battery can sustain some 1,500 cycles.

mechanisms is the fact that they do not start spontaneously but only under specific conditions. Unless there some "seeds" (e.g. dust particles) are present water vapor can remain in the gas state well below 100 degree Celsius (at atmospheric pressure); similarly liquid water can remain liquid well under zero degree Celsius. As a matter of fact, the "seed" can take different forms. For instance supercooled water (i.e. liquid water under zero degree) will freeze when one adds a tiny piece of ice but not when one adds a tiny piece of chalk. A sudden vibration produced by a mechanical device can also induce freezing. As a matter of fact, experiments show that the onset of freezing is for a large part a random process that cannot be predicted with certainty. This leads us to an important distinction.

Equilibrium versus non-equilibrium

The investigation of any transition phenomenon $A \longrightarrow B$. whether it is physical or non-physical, involves two parts.

(1) The study of the equilibrium situations A and B.
(2) The study of the time-dependent process which leads from A to B.

As a rule, part (1) is much simpler than part (2)[11]. This rule was just illustrated by the case of the condensation and solidification of water. For the equilibrium states there is a simple rule, namely:

$$\text{temp.} \leq 0 \text{ degree: ice}, \quad 0 \geq \text{temp.} \leq 100 : \text{water}, \quad 100 \leq \text{temp.: vapor}$$

On the contrary, the transitions $A \longrightarrow B \longrightarrow C$ are complicated processes which, even now, are not well understood. That is why, below, we will also start our investigation with a discussion of the equilibrium states.

Condensation

It has been stated above that aggregation results from a competition between attraction and agitation. Let us start with a gas. We know that in such a system agitation dominates attraction. As in any physical system agitation is determined by temperature, if one assumes that temperature is kept constant it will be possible to bring about aggregation by increasing the attraction. As attraction forces decrease with distance, this means that we must reduce inter-molecular distances. This can be done by increasing the number of molecules per unit of volume. Such a system can be described with good approximation by the equation of state of a (classical) ideal gas: $pv = nRT$, where p is the pressure, v the volume, n the number of moles, R the gas constant (8.3 J/Kmol), T the absolute temperature. If T and v are kept constant and n is increased it means that the pressure of the gas will increase. At some

[11] A a matter of fact, some important parts of physics such as statistical physics, apply only to equilibium (or quasi-equilibrium) situations. It is true that there is also a field called non-equilibrium statistical but it is beset with many difficulties; even as important a notion as temperature cannot be defined in a system which is out of equilibrium.

point the inter-molecular distance will become small enough for the attraction to balance the agitation; then condensation will take place. Can we put this argument into quantitative form and predict for which inter-molecular separation condensation will occur? The answer is yes. The calculation is given in Appendix A and the results for water and ethanol are shown in Fig. 1.

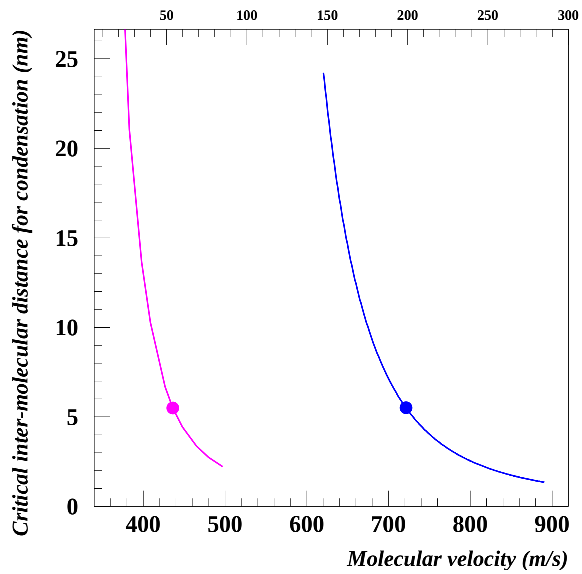

Fig. 1 Condensation of a gas into liquid droplets. The blue curve is for water whereas the magenta curve is for ethanol. The dots correspond to a pressure of one atmosphere. The corresponding distances are almost the same as could be expected from formula (A1). *Source: The data for the vapor pressure of water were taken from Rankin's formula; for the vapor pressure of ethanol the data are from the Wikipedia article for ethanol.*

Aggregation in bacteria populations

This is not a new question. As a matter of fact, early studies appeared as early as 1924 (Jahn 1924).

Aggregation processes in populations of myxobacteria and in Dictyostelium discoideum, a species of soil-living amoeba, have been actively studied by microbiologists (at least) since the mid-1970s. One of the reasons of this interest was the fact that aggregation occurs together with cell differentiation as is illusrated in the second and third row of Fig. 2. Among the facets that were most studied one can mention the genetic aspects and the identification of the chemicals which induce and control the aggregation process. Needless to say, the details of these processes are not the same for different species. It seems that only few studies tried to identify a core-pattern that would be common to a whole class of cases.

It would be a simplistic view to think that the aggregation process always starts in response to starvation (as is often stated) and that, once begun, it goes through the same steps. A closer examination shows two features which have close parallels in

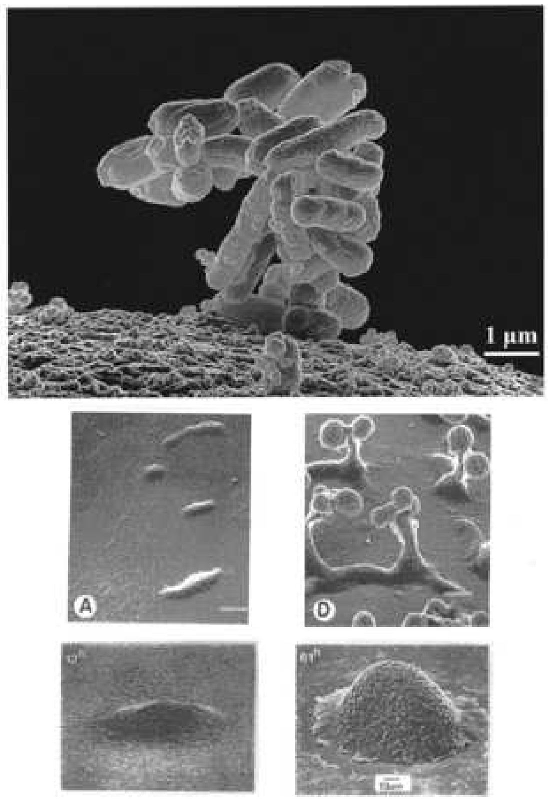

Fig. 2 Aggregation and clustering in bacteria population. The picture in the first row shows a cluster of some 30 Escherichia coli bacteria. the picture in the second row shows two stages in the formation of so-called fruiting bodies of a myxobacterium, *Stigmatella aurantiaca.* The time interval between the two stages is about 30 hours. The spherical shapes on top of the formation contain spores which can give rise to bacteria when conditions become favorable. The height of the little "trees" is about 0.1mm which means that it contains a large number of the 1-micrometer long bacteria. The third row shows two stages in the aggregation process of a myxobacterium, *Myxococcus xanthus*, which are separated by a time interval of 50 hours. The spherical formation is about 0.1mm high and comprises mostly spores. The aggregation process was started through a concentration of 10^{-3} mole per liter of calcium chloride. In contrast, replacement of the nutritive medium by water failed to start the aggregation process. *Source: First row: Wikipedia article entitled "Microorganismes" United States Department of Agriculture (image in the public domain); second row: Stephens et al. (1982); third row: Kuner and Kaiser (1982).*

the phenomenon of micelle aggregation.

- Most often for the aggregation to start the concentration of specific chemicals must be high enough. Thus, no significant aggegation occurs for *Stigmatella aurantiaca* unless the calcium concentration is higher than 0.2 millimole per liter (White et al. 1980, table 1) It can be recalled that the process of micellisation is also much affected by the concentration of sodium chloride (or other coumpunds).
- Assuming that an aggregation process takes place, the shapes of the aggregates are highly dependent upon the chemicals which are present. Thus, if the concentration of magnesium is too low, the fruiting bodies will have no stalks. In this case he heads of the aggregates (the so-called sporangia) rest directly on the little "hills" of

bacteria that were formed in the first stage of the process (White et al. p. 402).

Aggregation in insect populations

In their famous book about ants, Hölldobler and Wilson (1990) write: "Ants, like other social insects have a universal tendency to aggregate. [. . .] If a group of workers are taken from their nest and placed in a separate container, most will soon coalesce into tight clusters. [. . .] An exceptionally simple system of attraction exists in fire ants of the genus *Solenopsis*. When away from the nest and in close quarters, workers attempt to move up carbon dioxide gradients, hence in the direction of the largest nearby clusters of ants (Wilson 1962, Hangartner 1969)."

These excerpts represent fairly well both the strength and weaknesses of studies concerning aggregation in insect populations. For instance, the last sentence conveys the impression that carbon dioxide concentration plays a key-role in the aggregation of ants. However, what is shown in "Wilson (1962)" is a much weaker result than what is claimed in this sentence. The experiment showed that when given the choice between a test tube containing only air and a test tube that had been filled with carbon dioxide, in 80% of the 20 replications the ants entered into the second tube. The article makes clear that "as the rate of diffusion [of carbon dioxide] was not measured the procedure is not precise enough to indicate the optimum concentration". The fact that ants are attracted by low concentrations of carbon dioxide is not surprising for it has been shown that the concentration of carbon dioxide in ant colonies is about 1%-2% that is to say some 40 times higher [12]than in air (Portier and Duval 1929, Raffy 1929). Therefore one can understand that ants "feel more at home" in a test tube with a low (yet unknown) concentration of carbon dioxide. However, this does not mean that carbon dioxide is the only factor in the attraction between ants.

Aggregation in social systems

Examples of political integration

In 18th century Germany there were about 400 sovereign entities: kingdoms, principalities, bishoprics and other ecclesiastical states, free imperial cities, and so on. Many of them had their own currency, army and custom offices. One century later they had all coalesced and formed the German Empire.

At about the same time the different political entities which existed in Italy coalesced by forming a unified kingdom. It is true that the Vatican retained its independence. Its situation is somewhat similar to the principality of Monaco in near Nice in the South of France.

[12]This is hardly surprising because the "engine" which allows the physical activity of ants basically burns sugar and relieses carbon dioxide.

While these aggregation processes were under way other countries simultaneously experienced disintegration processes. One can mention Austria which became Austria-Hungary in 1867 after the Austrian defeat in the Austro-Prussian War (1866), Denmark which successively lost Norway, Schleswig-Holstein and Iceland or the Ottoman Empire.

Can these evolutions be interpreted in terms of attraction and dispersion forces as in previous examples. The answer is ‘yes”. Indeed when looking at it from a distance the evolution becomes fairly clear.

Binding forces shift from religion to language

Before the middle of the 18th century, the “binding energy” of countries and states was their religion. At that time all strong states had but one religion. For instance, in order to apply for British citizenship the applicant had to accept the doctrine of the Anglican Church about transsubtantiation. Politically, this situation was highly detrimental to the “Holly Roman Empire” because the Lutherian and Calvinist reforms of the 16th century had broken religious unity.

Then, during the late 18th century for a number of reasons that we do not wish to discuss here, language together with a common culture progressively became the “binding energy” of states. Within one century this brought about tremendous changes:

- Unification of Germany as we already mentioned, but also of Italy.
- Disintegration of Denmark (which had included Norway, the southern province of Sweden, Iceland as well as parts of Germany), of the Austrian Empire, of the (Turkish) Ottoman Empire.
- The unification of India can be seen as dual process in which both religion and common cultural heritage played a role.

It is true that the the previous explanation does not account for all observed facts. For instance it does not explain why Spanish-speaking Latin American countries or Middle Eastern Arabic-speaking countries did not form single political entities. At the other end of the spectrum, this explanation does not explain the existence of a country such as Switzerland which has neither a common religion nor a common language. However, it should be observed that Switzerland is a confederation, that is to say a fairly weak and loose form of state that leaves even more autonomy to its provinces (in this case the so-called Swiss cantons) than a federation. Its duration and stability makes Switzerland a fairly unique case. Geography may have been a crucial factor in the the fact that Switzerland was able to maintain its identity for so long and without any major upheaval.[13].

[13] In Rahilly and Roehner (2002, p. 172) it was shown that war plays a crucial role in revealing separatist feelings. In a more general way, this book provides a more detailed discussion of this issue. The comparison between Belgium and Switzerland is quite revealing in this respect.

Regarding the case of Middle Eastern countries, it can be recalled that some merger attempts did occur. For instance, Egypt and Syria formed the short-lived United Arab Republic (1958-1961) or the failed attempt of the Arab Islamic Republic which involved Libya and Tunisia in 1974. An important factor in the failure of many merger and unification plans is the disruptive influence of the great powers.

"Divide et impera"

The Latin expression *Divide et impera*[14] means "Divide and rule" with the implication that breaking up opponents is a good strategy for gaining and maintaining power. Many illustrations of this strategy can be found in the history of past centuries. A fairly recent example was the support given by India to the secession of Bangladesh from Pakistan.

One again, there are apparent exceptions. For instance, at first sight it may seem surprising that in Germany the policy of Napoleon on the contrary favored unification. The explanation is that this policy was directed against Prussia which (together with England) was Napoleon's most persistent opponent. The purpose of the unification process among German states which were Napoleon's allies against Prussia was to form a bullwark against Prussia. As the history of the following century would demonstrate, such a plan attested quite a lucid foresight.

Integration of ethnic groups

In the previous examples the different components had a clearly defined diplomatic identity. A similar process is the melting-pot mechanism through which immigrants become integrated in the country in which they choose to settle. As one knows, this process played such a major role in the formation of the United States. From a statistical perpective, groups of immigrants can be identified as foreign nationals but only until their naturalization. However, in the United States the integration of groups of immigrants can be followed in statistical yearbooks even after they have been granted US citizenship because US statistics provide information about the *country of origin* of second- or third-generation immigrants. On this question more details can be also be found in Rahilly and Roehner (2002, chapter 5).

Aggregation experiments with insects

Our own questioning started in 2011 when we came across a series of papers written by a French entomologist, J. Lecomte (1949,1950,1956). The papers describe the phenomenon of cluster formation in bees in a way that was new in two different ways:

[14] Other forms which have basically the same meaning are *Divide ut imperes* or *Divide ut regnes*.

- Previously (and even subsequently) entomologists had mostly focused on the means of communication without paying much attention to the effectiveness of the dynamic of the clustering proces. In contrast, Lecomte studied carefuly the conditions under which clustering takes place.
- Beekeepers are familiar with the kind of clustering that occurs in a number of circumstances such as cold weather, or the formation of a swarm before leaving the beehivehe but the experiments done by Lecomte showed that aggregation was a basic behavior of bees which take place without any external stimulus as soon as a sufficient number of bees are held together in a limited area.

More spefically, Lecomte demonstrated the following points.

(1) A clear aggegation pattern (with the formation of only one cluster) requires a number of bees larger than a crtical number which is of the order of 70 for a box of same size as a beehive (i.e. about

(2) The time constant of the clustering process is approximately one hour and a half.

(3) Clustering occurs whether the bees belong to the same colony or to different colonies

Incidentally, Lecomte also writes that between 15 and 30 degree Celsius aggregation is little affected by temperature, which is completely at odds with our own observations. Indeed, we observed that the formation of a cluster is about three times faster at 26 degrees than at 16 degrees.

Appendix A: Condensation

A gas at a temperature T_c starts to form droplets of liquid when its pressure reaches the saturation pressure p_c of the liquid at that temperature. Thus, when the pressure of nitrogen kept at a temperature of -196 degree Celsius is raised to 10^5Pa (i.e. standard atmospheric pressure) the molecules of the gas start to coalesce into droplets of liquid (at least if "seeds" are present as explained at the beginning of the paper). To the pressure p_s corresponds a specific average separation r_c that can easily be obtained from the state equation [15] $pv = nRT$. If one takes $n = 1$ mole, $v = N_a v_1$ where, N_a is Avogadro's number and v_1 the volume alloted to each molecule. Recalling that $R = k.N_a$ where k is Boltzmann's constant, one gets: $v_1 = kT/p$. If we denote by r_c the side of the cube v_1, the distance between the centers of two adjacent molecules will also be given by r_c. Thus $r_c = (kT_c/p_c)^{1/3}$

[15] It is for the sake of simplicity that we use the state equation of an ideal gas; for a gas near its condensation point the van der Waals equation of state

$$\left(p + \frac{a}{v^2}\right)(v - b) = kT$$

would be more appropriate.

The relation which gives p_c as a function of T_c is specific to each gas but can be obtained from the Clausius-Clapeyron formula. There are several forms of this formula and for the present case the most convenient is: $p_c = C\exp(-L/RT)$, where L is the heat (or enthalpy) and C a constant given by $C = p_1\exp(L/RT_1)$ where (T_1, p_1) is any point of the condensation curve, for instance the critical point, i.e. the point for the highest possible temperature. of vaporization. Replacing in the equation above, one gets:

$$r_c = \left(\frac{}{C}\right)^{1/3}\left[T^{1/3}\exp\left(\frac{L}{3RT}\right)\right] \tag{A1}$$

Let us first consider this equation for a given gas. What happens when we raise the temperature. The two factors $T^{1/3}$ and $\exp(L/3RT)$ changes in opposite direction. The first increases while the second decreases. However, the second factor changes faster than the first [16] . Consequently, r_c must become smaller in order for condensation to occur. This makes sense. If molecular agitation increases, the attraction must become stronger for aggregation to take place.

Now, we wish to consider two different gases at the same temperature. As an illustration, we take ethanol vapor and water vapor as in Fig. 1. The heat of vaporization L is a measure of the molecular interaction strength because it is the amount of energy that is required to break molecular bonds. As ethanol has a lower boiling temperature than water we also expect its heat of vaporization to be lower. Indeed for ethanol $L = 38.6$kJ/mol. This means that for the same temperature the condensation of water will take place for a larger inter-molecular spacing than for ethanol. As an illustration, $T = 300$ gives $\exp(L/3RT) = 175,\ 232$ for ethanol and water respectively. In fact, Fig. 1 shows that the real difference is even larger.

In this simple argument we forgot that L in fact changes (slightly) along the condensation curve. We also omitted the fact that the facor C is not the same for different gases[17].

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[16] Suppose that in the case of water T changes from 400 degree Kelvin to 500. $T^{1/3}$ will change from 7.2 to 7.7, i.e. 8%; in contrast, with $L = 40.6$kJ/mol and $R = 8.3$J/mol, $\exp(L/3RT)$ changes from 55 to 25, i.e. 56%.

[17] However, in a $1/T, \ln(p)$ graph, the condensation curves for different gases are almost straight lines (of slope $-L/R$) which more or less converge toward the same point on the left-hand side of the graph that is to say on the side of the critical point. This shows that the magnitude of change of p with respect to T for a given gas is much larger than the changes in the (T, p) coordinates of the critical points of different gases.

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[18] *Apis mellifica* is the same species as *Apis mellifera*. In Latin the meaning of "mellifera" is "to bear honey" whereas the meaning of "mellifica" is "to make honey" which is of course more correct because indeed bees absorb nectar and deliver the honey only once they come back to the beehive.

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