

TOWARDS A MODEL OF HOST-PARASITE RELATIONSHIPS

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ABSTRACT

The question asked in this article is: "what is a parasite?". Defining a parasite requires defining its host at the same time. A difficult question therefore arises about host-parasite relationships. The object of general parasitology is in fact to study the relationship between a host and its parasite. The initial question "what is a parasite?" has to be reformulated within a conceptual framework, that of "relationship". This article is an attempt to transpose into parasitology some concepts which have been profitable in the fields of physics and chemistry. The studies of R. Thom about the individual are also used. Concepts like that of field and principles like that of minimization are probably operational on a high level of organization. The description of host-parasite relationships could benefit from these concepts.

1. INTRODUCTION

"What is a parasite?" This question may be considered inappropriate. Everyone knows what a parasite is! But it is difficult to define a parasite without defining its host, and the initial question has to be reviewed within the framework of relationships between two beings. For example these relationships consist of trophic, immunological and ethological interactions. Once established, the host-parasite association is solid: it is difficult to eliminate the parasite from its host.

How can a large framework be defined in which parasitism seems to be a specific case? Parasitological association refers to the concept of coupling. The meaning of the question "what is a parasite?" would then be: "what characterizes host-parasite coupling in a general coupling model?"

2. COUPLING

Various levels of coupling in host-parasite relationships

The concept of coupling in parasitology occurs on several levels. The image which comes most easily to mind is that of the coupling of one host and one parasite. On this level, the questions are: How can these two beings coexist without one not destroying the other? Why is it so difficult to drive the parasite away from its host? How can parasitic specificity be explained? How can the terms pathogenicity and susceptibility

be defined? Which criteria should be used to distinguish commensalism, parasitism and symbiosis?

On a higher level of organization, the developmental cycle of a heteroxenous parasite must be coupled with a predation cycle or with some specific way of life which can ensure transmission from one host to another. The predation cycle of hosts and the life cycle of parasites have to be synchronized: for example, a cysticercus remains a cysticercus until swallowed by its definitive host; it then becomes a taenia. Populations of hosts and parasites are reciprocally controlled. There is a dynamic equilibrium between these populations. The questions can be expressed in quantitative terms i.e. in terms of population size. Thus, mathematical models using systems of differential equations can be applied.

On levels of organization more specific than the organism itself, the questions are about the way the parasite circulates within its host, or about the choice of such and such an organ or cell as target. Sometimes, the description level is not obvious: if a protozoan parasitizes a metazoan, what is the relevant level: cellular level or parasite population and host organism level? What is the relevant level of description for an intracellular parasite in a metazoan?

On the molecular scale too, interactions and coupling have been highlighted between molecules or systems of host and parasite molecules.

In this article, a general model is sought to describe the concept of coupling. Thus, this model must be relevant regardless of the description level and must form a framework inside which the questions asked can be reformulated. A geometrical model rather than a quantitative one is sought to describe coupling. The required model is a geometrical representation allowing for continuous deformation to describe the continuous passage from commensalism to symbiosis through parasitism. The search for such a model is a vast task which cannot be accomplished in a short space of time. The present article will simply try to open up some ways. Its principal concern will be the coupling of two individuals, a man and a taenia for example.

Coupling and the concept of the individual

One of the difficulties with which biologists are confronted is the definition of levels of hierarchical organization, related to the definition of the individual. The following definition may be a starting point: an individual is a set of elements interacting among themselves and with the environment. The interactions cannot be represented by material localisable entities; they are of the same nature as a field in physics. Thom (1975, 1980, 1986, 1988, 1990) uses the word "prégnance" in French, the nearest translation of which would seem to be pregnancy, to indicate these non localisable entities. There are, therefore, strong interactions between the components of the individual (this is what ensures the individual of his or its own individuality) and weaker interactions between the individual and the environment. Described as such, the individual (etymologically an "atom" synonym) can be a cell or a being or a population or a molecule. The hierarchical levels are defined according to the importance of interaction forces. There are discontinuities in the bond energy levels, and so various levels of hierarchical organization. It should be noted that physicists no longer say "elementary particle" but speak about the physics of high energies (Pascaud, 1989). The idea of describing beings in terms of "elementary particles" which would be molecules, is probably a utopian view; there is probably no

irreducible level. Molecular biologists would be tempted to study and understand life on a more specific level than the molecular one, supposedly a more fundamental one.

Prey-predator, host-parasite, symbionts; a continuum of relationships

Host-parasite relationships are a challenge for general parasitology. The question which is asked is: "How can two beings which are thought of as two distinct individuals be coupled so that they make a whole which is indivisible into its parts?" The host-parasite couple is a whole - this is essential. If we understand parasitism as a trophic relationship, then the concepts of whole, part and coupling can be made clear. Couples are to be found in three cases: predator-prey, host-parasite, symbionts. In predation, the parts dominate, but they exist only at the beginning of the phenomenon; later, the predator eats and assimilates its prey. In symbiosis, the whole dominates: symbiont relationships are symmetrical. There is only one word (symbiont) to designate the two individuals of the couple. It is remarkable, from this point of view, that the lichens which are a paradigm for symbiosis, have genera and species names in botanical classification. The components, alga and fungus, are subordinated to the whole which is lichen. In parasitism, the situation is more ambiguous. The host and the parasite appear as two individuals; they are two "wholes". Each individual has its genus and species name. But host and parasite are also parts of the host-parasite couple.

The host-parasite couple is a "whole"; this has to be exemplified. When an individual (the host) is parasitized, energy has to be spent to separate the two parts of the couple: vermifuge drug is needed to eliminate worms from a cat. A host-parasite couple is a whole, so parasitic disease therapy is difficult. The difficulties would be greater if host and parasite could be separated and kept alive. We are usually satisfied when we destroy the parasite. The "whole- part" relation in the host-parasite couple is similar to that which exists between organ and organism. A healthy cat, for example, is a whole. By thought experiment, it can be broken up into parts, its organs. By a concrete experiment, organs can be separated from the organism or rather destroyed: an animal can be castrated, for example. Similarly, a parasitized cat is a whole. By thought experiment, this whole can be divided into parts, cat and worm, or by concrete experiment the worm is killed with a vermifuge drug; to do that, energy is used. Let me be provocative and ask: "what is a man?" This question can be more specific: "Is the intestinal flora a part of the man? . In other words, is an axenic man a man?"

Within the framework of immunology, similar difficulties arise to define the individual, the whole. It would be pleasant to regard the host as a whole, the "self", which rejects another whole, the "non-self". The facts are different; the host-parasite couple which forms a whole, is difficult to dissociate; "self" does not reject "non-self". Capron and Dessaint (1989) underline this difficulty in connection with vaccinations against parasites, "*the reasons for our present failures are no longer attributable to the lack of appropriate tools but rather to our rather primitive knowledge of the basic mechanisms governing host-parasite relationship*".

Parasitism is a sort of relationship between beings which denies the concept of the biological individual. Strictly speaking, a parasite does not have real biological individuality, because it can only live at the expense of another individual. The parasitized host also loses its own individuality because it cannot generally throw off its parasite. A paradox could be used: "a parasite is not a being". Think of the viruses which are now being considered from this point of view. Some people think this is a

useless philosophical discussion. But in fact, this controversy indicates that this crucial problem must be formulated within an appropriate conceptual framework to solve any difficulties encountered.

3. INDIVIDUAL AND INDIVIDUALISING

Coupling of a priori elements

This section takes its inspiration from chemists' definition of the coupling of two or more atoms which are considered as elements to constitute a molecule (Grecias and Migeon, 1989).

Above, an individual was considered as a set of elements in interaction, as a set of coupled elements. The definition of the elements can be an obstacle: what is now considered as elements may be made up of smaller elements on a further analysis; atoms in physics is such an example. To progress more quickly, the elements will be considered a priori and will be thought of as points in ordinary space. The simplest system to be built, under these conditions, consists of two points A and B.

Two independent elements, A and B; configuration space

Consider first that each point A and B is located in space by three numbers, the co-ordinates of the point. These six co-ordinates used to describe the state of this set of points are not independent; in fact the state of a system made of two points is described by only one number, that is distance AB. The following question is: "when can two points be called independent or coupled?" To answer this question, a model is built; this model is made up of a point which moves on a line, or more precisely on a half-line (Ox) because a distance is positive. The abscissa of this point is the distance AB, that is, the abscissa represents the state of the system. The half-line Ox is named "system configuration space".

Coupling of two elements A and B; bond

The question: "when can two points be called independent or coupled?" is now translated through the model and becomes: "when is the state of the system called free as opposed to constrained?" The state of the system is said to be free if its representative point invades all the configuration space over a rather long observation time. The system will be said to be very strongly constrained if the representative point does not move in the configuration space. In this case, the two elements of the system, the two points A and B are at a fixed distance from each other, they are bound. Between these two extreme situations, there is a very great number of possible variations. For example, the representative point can remain in the neighbourhood of a fixed point P_0 . This situation is interesting, because it suggests the existence of a regulating mechanism, of a "force" which brings back the representative point to P_0 when a disturbance moves it away. This behaviour can be checked experimentally. The initial model can then be developed and a field of potential added to the configuration space, so that this potential presents a minimum in P_0 . The behaviour of the system is governed by a minimization of potential. Figure 1 shows such a model: when the distance AB is large, the point representative of the system is in a very flat basin of the potential curve, the system is practically free, points A and B are not

dependent. If the distance AB decreases, the system crosses a barrier of potential (a maximum on the curve) and the representative point sinks. The system remains in a state close to P_0 , the points A and B are dependent on each other. The two points make up an individual in the same way as two bound atoms make up a molecule in chemistry.

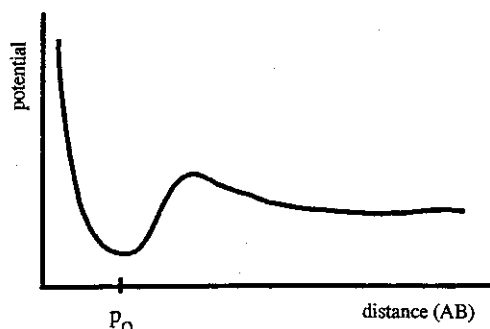


Figure 1. Distance is controlled by potential minimization.

However, the system may not present this stability property: the point P_0 is fixed, but after a disturbance it remains in the new imposed position. The system may still be multistable: there will then be a finite number of points P_i ($1 < i = N$) which behave like P_0 and around which the state of the system can stand. The field of potential then presents at most N minima.

Coupling of three elements A, B and C; progressive abolition of the degrees of freedom, structure levels

A system is now considered which is made up of three points A, B and C in ordinary space. The configuration space is three-dimensional. The choice of the co-ordinates in the configuration space is arbitrary; the distances AB and AC and the angle BAC may be chosen, for example. Let us first suppose that A and B are dependent and that C is independent. The representative point of the system is confined to a portion of the plane. If, in addition, A and C are dependent but not B and C (the distances AB and AC are fixed, but the angle BAC is variable), then the representative point is confined on a line segment. If the system behaviour is governed by a minimization of potential, then the portion of plane and the line segment are attractors of the subjacent dynamics.

Instead of specifying the significance of the axes of co-ordinates in the configuration space, a very general framework may be retained. It can be said that there is coupling between the elements if the representative point is confined to the neighbourhood of one or of a finite number of subvarieties of the configuration space: the couplings correspond to topological constraints. For an unspecified choice of co-ordinates in the configuration space, the significance of these subvarieties will not be obvious. A judicious change of co-ordinates will enable interpretation in ordinary space. Imagine, for example, that A, B and C are three amino acids. The preceding connections AB and AC are peptide bonds. If the angle BAC is free, the situation is that of primary structure description. By fixing the angle BAC, the secondary structure is then described. An interpretation may not be so immediate for

another choice of co-ordinates in configuration space: two of the angles of the triangle ABC and the radius of its circumscribed circle, for example.

Coupling and individualising

The concept of coupling introduced previously can be extended to a great number of elements: there is coupling between elements if the representative point of a system made up of a set of elements does not completely invade the configuration space. Coupling corresponds to a reduction in the number of degrees of freedom. It seems that the coupling condition is necessary but insufficient to describe the individual. A stability condition is also necessary. There must be a dynamic, a field in the configuration space which ensures the regulation of the individual. The following proposal is made: a set of elements constitute an individual if the representative point of the system is retained in the neighbourhood of a subvariety of the configuration space by dynamics.

Salience and pregnancy; individualizing pregnancy

Salience and pregnancy are terms introduced by Thom (1975, 1980, 1986, 1988, 1990). In physics, these concepts correspond to those of particle and field. Like a particle, a salience is a discontinuity which is localisable in space and/or time. In space, an object, a ball for example, is a salience. The tinkling of a bell is a salience in time. Topologically, a salience is a closed set. A pregnancy is not localisable; it tends to invade space, it has spreading properties. When a pregnancy invades a salience, figurative effects are produced. Light and heat are examples of pregnancies. When heat invades a piece of ice, ice melts. Each scientific domain studies a small number of saliences and pregnancies and tries to specify the laws which govern the propagation of pregnancies by studying the figurative effects. In mechanics, saliences are material bodies, pregnancies are energy and momentum; propagation of pregnancies is governed by the principle of the least action, figurative effects are accelerations. In chemistry, saliences are molecules, pregnancies are local interaction potentials, propagation is carried out by diffusion and figurative effects are the concatenation of molecules (Thom, 1986). In this formalism, Thom (1988) considers the concept of the individual and the process of individualising. His concern is to solve or rather to pose the problem correctly. Individuals are structured forms in space. This structured morphology induces a splitting up into component parts. For example, the human body can be split up into organs; these parts may be represented in a graph (Thom, 1988) (Figure 2). This splitting up is not arbitrary, it mimics the embryogenic process. On this graph, arrows go from the "human body" but none end here. "The human body" is said to be a source form for an individualizing pregnancy of individual. This pregnancy is represented as a crater of potential. The source form is at the minimum of potential and the graph is along the valleys on the crater. The crater itself is bound by a ridge corresponding to the individual edge. The potential is the pregnancy which is the individual regulatory principle. This is a more general representation of Figure 1. The source form is a salience which is a singularity of an individualizing pregnancy.

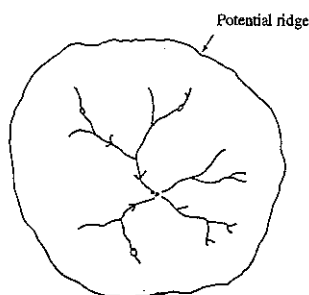
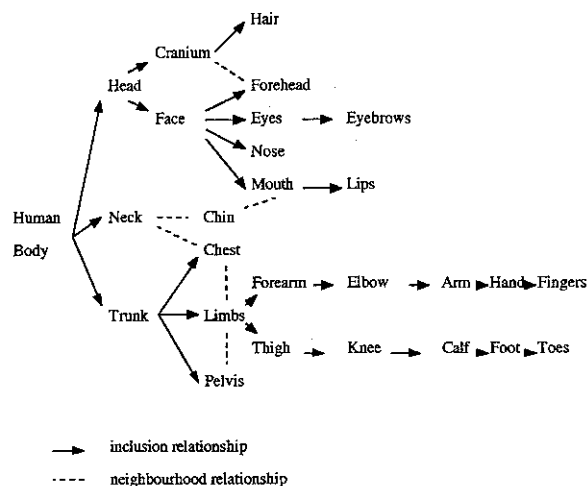


Figure 2. Graph of human body splitting up and its interpretation (translated from Thom (1988)).

Individual and hierarchical level of organization

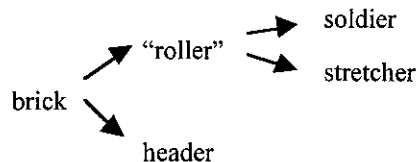
Hierarchical level of organization and degree of freedom.

The structure of proteins is familiar to biologists and may be chosen to illustrate the concept of individual and hierarchical organization. Take a protein made up of n amino acids. To describe its structure, in a first approximation, the amino acids are thought of as points. Protein structure is then described as the relative positions of n amino acids, using one point in a configuration space with $(3n-6)$ dimensions. If the n amino acids effectively constitute a protein, they are dependent and the representative point does not invade all the configuration space. Now, the question is: what are the primary, secondary and tertiary structure levels of the protein in the configuration space? The primary structure describes the sequence of the amino acids. The distance of each amino acid from the previous or the following is fixed; the configuration space of the protein, with these new constraints (imposed distances between amino acids) is a $(2n-2)$ dimensional space. So, the description of protein primary structure constrains the representative point to move only inside a $(2n-2)$ dimensional variety embedded in

the $(3n-6)$ dimensional space of positions of n points. The secondary structure individualizes portions of the sequence (the primary structure) by fixing the relative distances of amino acids inside groups which constitute an alpha helix or a beta sheet. The representative point is thus constrained to move on a variety with a rather restricted number of dimensions, much lower than $(2n-2)$. The number of degrees of freedom corresponds then to possible relative displacements of the new units individualized by the secondary structure. The same reasoning continues for the description of domains and tertiary structure.

Super-individual by union of basins

Protein configuration is governed by energy minimization. To each point on the configuration space corresponds a potential energy of the system. The stable configurations of a protein correspond to the lower minima. If the system is disturbed (that is, if energy is applied), the representative point visits the basins of several attractors (local minima). The more significant the disturbing energy is, the more numerous the basins visited; the number of degrees of freedom of the system increases. The levels of hierarchical structure correspond to the disturbing energy levels producing an abrupt increase in the number of degrees of freedom, i.e. allowing for the crossing of a great number of barriers of potential located at approximatively equal levels. Another example chosen in a two-dimensional configuration space make this clearer: a pebble collected on a beach is not perfectly spherical. When it is set on a horizontal level, it remains in equilibrium. This position corresponds to a local minimum of potential energy (the centre of gravity is as low as possible). How can the pebble position be located? The configuration space (= the space of the pebble position) is two-dimensional: the pebble position is located from its surface point (a two-dimensional object) which is in contact with the horizontal level. Observation of this configuration space shows that there are several equilibrium positions, each one corresponding to a local minimum of potential energy. Each stable position is surrounded by a basin of attraction, constituting a facet on the surface of the pebble. Applying some energy to the system by shaking the horizontal level more or less vigorously, for example, can roll the pebble from one facet to another by crossing the barrier of potential energy that is a facet edge. If the imparted energy is weak, the pebble rolls on a set of facets, not around all the facets. A facet, in the nondisturbed system has to be considered as an individual. In the disturbed system, a set of facets represents a new individual. The heights of the energy barriers create a structuring, a hierarchical organization of the sets of facets. For a better explanation, replace the pebble with a brick. With low disturbance, the brick ends up resting on its most extended face, the soldier in technical term. With more significant disturbance, the brick moves on a set of facets (soldiers and stretchers). With even greater disturbance, the brick rolls on all its facets. There is a hierarchical organization of the brick surface:



This graph is similar to that of the decomposition into parts of the human body. In the example of the brick surface, the potential can be indicated explicitly - it is potential energy. In the configuration space, each facet is the neighbourhood of a point (dimension 0), the "roller" is the neighbourhood of a line (dimension 1), the whole surface is two-dimensional. The edges on the pebble correspond to crest lines in the potential crater and the hierarchical structuring can be understood as the union of several basins of attraction when the crater fills (imagine the level of water filling it). Several individuals (facets) meet in a super-individual by clearing the barriers of potential by means of disturbing energy. Now, let's turn again to proteins: the individual could be an allosteric configuration, or a set of configurations or the protein in varying degrees of denaturation, down to its primary structure. Note also that the shape of the potential crater is under the control of environmental parameters (surface-active agents or pH for example). This situation can be mimicked, in the case of the pebble, by modifying the position of the centre of gravity (if the pebble is made up of nonhomogeneous matter). So, the changes in structure imposed by external parameters became clearer.

Self and non-self

Self and non-self are concepts very frequently used in immunology, but immunologists do not have explicit models of these concepts. Implicitly, "self" and "non-self" are thought of as material localisable entities, as saliences in the vocabulary defined higher. The concept of the individual has been discussed and the concept of individualizing pregnancy has been introduced as a field which ensures the cohesion of the individual. The following proposition may now be made: "self" is the way by which individuality exists, rather than the individual himself; in other words "self" would be a pregnancy. "Self" may also indicate a salience, the individual, but it should then be regarded as the source form of this individualizing pregnancy "Non-self" would be a salience. By analogy with field and particle (taking the example of gravitation), "self" is the analogue of the gravitation field, antigen is the analogue of a material point: A gravitation field can be detected by using a material point as a testing body. The material point allows for gravitational field detection through a figurative effect, an acceleration. In the same way, an antigen can detect the presence of "self" (the field, the pregnancy), through a figurative effect which is the immune reaction. In physics, several particles (source forms) may be replaced by a field. In the same way, the "self" field may replace all the elementary immunological mechanisms and their material supports. In physics, a field is also the memory of what has occurred in the space that supports the field. The "self" field is also a memory in immunology. This "self" manner of thinking should encourage the search for laws of the same type as the laws of physics, to find an equivalent of the law: $F=mg$. This requires that the nature of the space which supports "self" should be elucidated and that the mathematical object (scalar, vector...) suitable to describing the field at each point should be found. This however, is not the object of this article.

Parasitology is interested in the interaction of two "selves" whose source forms are the host and the parasite. It is thus interested in the interaction between two fields (not of a field and a particle), because the parasite is more complicated than an antigen.

4. ANALOGIES

If parasitism is to be thought of as a mode of trophic relationship, the parasite will be placed in a food network. This network will be represented as an oriented graph. The nodes of the graph are the species composing biocoenosis, the edges representing the relationship "eaten by". If this graph does not present cycles, it will be put in a potential crater like that of Figure 3. A food network is an individual controlled by an individualizing pregnancy. The substratum space is not easily specified. The simplest case is that of a food chain. Thus, by means of a thought experiment the species of the food chain may be classified in a one-dimensional space that is on a scale which goes from "very prey" to "very predator". This type of classification and scale evokes the acid-base or redox scales.

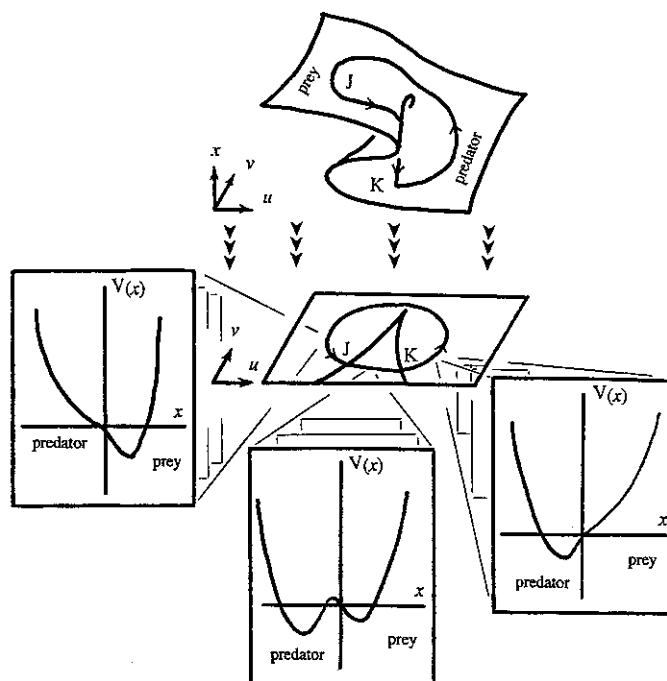
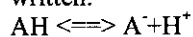


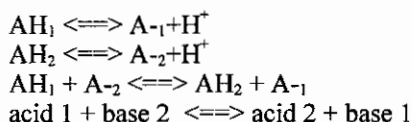
Figure 3. The predation loop and its interpretation.

Acid-base, oxidizing agent-reducing agent, prey-predator couples

In the Brønsted Acid-Base theory an acid is a "proton donor"; a base a "proton acceptor" (Grecias and Migeon, 1989). An acid-base reaction is an exchange of protons. Every acid has a conjugate base and vice versa. An acid is noted AH and its conjugate base is A⁻. The couple is noted AH / A⁻. The following reaction may be written:

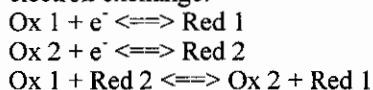


An acid base reaction is written as a sum of two half-reactions to show proton exchange:



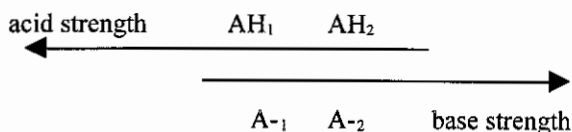
Water reacts with itself by transferring a proton from one molecule to another to form an H_3O^+ ion and an OH^- ion. So H_2O is an acid whose conjugate base is OH^- and H_2O is also the conjugate base of the H_3O^+ ion. H_2O is said to be amphoteric.

In the same way, an oxidation-reduction reaction is an exchange of electron. A reducing agent is an "electron donor"; an oxidizing agent an "electron acceptor". An oxidation-reduction reaction is written as a sum of two half-reactions to show the electron exchange:



There are also amphoteric chemical species for the oxydation-reduction reaction.

Acids are classified on a scale from strong to weak; one measure of acid strength is the acid-dissociation equilibrium constant. In this way, a scale for the strength of conjugate bases is also obtained, so the two scales are written one over the other:



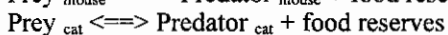
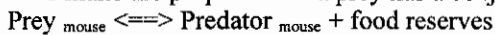
Similarly, couples of oxidizing agents and reducing agents are classified on scales.

The "predation reaction" and the predation loop

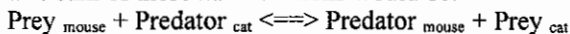
Above, acid-base reaction and oxidation-reduction reaction are presented within a theoretical framework. At present, teaching handbooks present all these things in a very theoretical framework (Grecias and Migeon, 1989). In fact, all of the oxidation-reduction reactions were known before they were understood as the sum of two half-reactions. The concept of strength in an oxidizing agent made it possible to classify these compounds on a scale and later to build a theory. Biology is still in a pre-theoretic situation. Animal species are classified on food chain scales, but a theory similar to that of Brönsted no longer exists for the prey-predator couple. An attempt to push the analogy further follows in the next section.

The prey-predator reaction

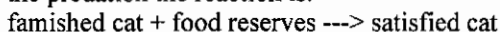
Let's make the proposition: "a prey has a conjugate predator". This is illustrated by:



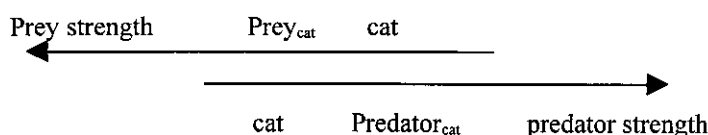
The sum of these half-reactions would be:



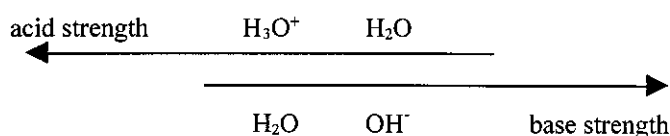
This sum is not appropriate for predation, but it could be acceptable for symbiosis. In the predation the reaction is:



If food reserves are the same as protons in the acid-base reaction, they should not appear in the reaction. On the other hand, mouse must appear. The reaction such as it is written, evokes the hydrolysis of strong acid in amphoteric water solvent. Thus, cat has to be considered either as the conjugate predator of the satisfied cat (Prey_{cat}) or as the prey of the famished cat ($\text{Predator}_{\text{cat}}$):



These scales have to be compared to the following:



Water has a limiting effect on the strength of acids and bases. All strong acids (such as HCl) behave the same in water: 1M solutions of strong acids all behave like 1 M solutions of H_3O^+ ion. HCl is said to be levelled by water. In the same way, within a cat, a mouse is levelled; a mouse is a strong prey, its conjugate predator is unable to collect the food reserves of cat.

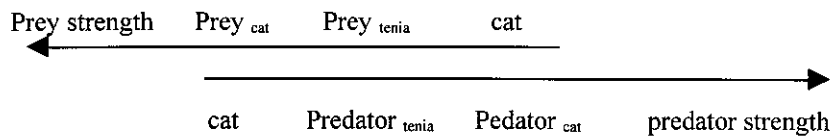
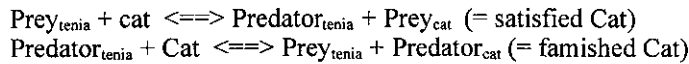
Predation loop

"Cat eats mouse" is the example chosen by Thom (1975) to describe the predation cycle. The difficulty that Thom tries to solve is to reconcile the irreversible character of predation and the permanence of the subject: "there are initially two agents: the subject, the eater (the cat) and an object, which is eaten (the mouse). At the end of the process, there is nothing but one agent, the subject (which triumphs over catastrophe)" (...) "However, it is necessary to develop this reflex into a periodic process, to be (indefinitely) repeated." (Thom, 1975). The solution suggested by Thom considers a process organized by a singularity and proceeding on a surface called cusp (surface of Riemann-Hugoniot) Figure 3. This surface represents in space $\{ X, u, v \}$ the locus of the minima and the maxima of the function $V = 1/4 x^4 + ux^2 + vx$. The x axis is a "predator-prey" axis, u and v are process control co-ordinates. V is a potential, a pregnancy which controls the state of the subject. During the story (cat eats mouse), u and v vary slowly and the $V(x)$ graph becomes deformed. The minima represent the individuals, the agents of the process. Just before the cat sees the mouse, $V(x)$ has one minimum located on the side "prey" of the x axis. This occurs at the point J on Figure 3, and this is the catastrophe of perception, as Thom named it. At this time, a second minimum appears. It is located higher than the previous one and for a "predator" value of x. This situation persists on segment JK, but the minimum "prey" goes up while the minimum "predator" goes down. After crossing point K, the minimum "predator" remains alone. It is the catch catastrophe. On the Riemann-hugoniot surface, that corresponds to the sudden jump from the top sheet to the bottom one. Then, on segment KJ, $V(x)$ gradually becomes deformed by preserving one minimum which moves towards "prey" on the x axis. At the end of the cycle, the

famished cat is on the prey sheet. According to Thom's expression, "the famished predator is its own prey". The sight of an external prey moves the representative point of the cat towards the metastable minimum of the predator. Cat becomes predator. This model was named predation loop by Thom; it describes the evolution of the cat state from a predominately predator state to a predominately prey one. In our opinion, these two states correspond to the amphoteric character of the cat. The x axis of the predation loop is replaced by the scale of the prey predator couple.

The parasite differentiated by its host

By analogy with the acid base couple, a parasite in its host is like a weak acidin-water solution (an acid differentiated in water). The prey-predator reaction, in this case, is an equilibrium and not a total reaction as in the case of predation. If a tapeworm in a cat is considered, it will be written:



The strength of parasites is differentiated by the amphoteric host. The greater the strength of Predator_{parasite}, the greater the parasite pathogenicity; in extreme cases, the parasite becomes a strong predator, equilibrium is broken. Conversely, the greater the force of the prey_{parasite} (the parasite is close to the couple Prey_{host} / host), the greater the susceptibility, if the capacity of a host to tolerate a parasite is named susceptibility. In most extreme cases, the parasite becomes a powerful prey and will be digested by the host.

In the model of the predation loop, the parasite appears as a middle sheet between the prey and predator states of the host; this layer corresponds to an additional minimum of the potential Vx. The present model concords with the idea of Audy (1958) that a parasite is a host tissue predator. The parasite behaves like a host organ: the organs of the host are small minima in the potential crater of its individualizing pregnance. This model has the advantage of giving significance (= to transform into signs) to the intuition of continuity from predation to parasitism.

5. CONCLUSION

Parasites have been studied by numerous methods. Increasingly acute knowledge has been obtained by very detailed analyses. The fight against parasites is becoming more and more effective. But difficulties remain and parasitism has to be examined in its general, fundamental aspects. For that, new images, i. e. models, are required. The reflections made in this article are an attempt to transpose into parasitology, some methods and concepts which have been profitable in the fields of physics and chemistry. The concept of field and the principle of minimization are probably operational on a high level of organization. But the development of such abstract tools

runs up against the concrete, standard modes of representation in the biological sciences. The place claimed here by abstraction may appear disproportionate compared to the absence of direct applications which are expected in the field of health, for example. However this will be worthwhile if questions about parasites (see Dujardin, 1986; Dujardin and Dei-Cas, 1990), can be expressed in a revised framework.

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REFERENCES

- Audy, J.R. (1958). The localizations of disease with special reference to the zoonosis. *Transactions of the Royal Society of Tropical Medicine* 52: 308-334.
- Capron, A. and J.P. Dessaint (1989). Molecular basis of host-parasite relationship: towards the definition of protective antigens. *Immunological reviews* 112: 27-48.
- Dujardin, L. (1986). Quelques concepts de dynamique qualitative utiles à la mycologie médicale. *Bulletin de la Société française de Mycologie médicale* 15: 469-472.
- Dujardin, L. and E. Dei-Cas (1990). Géométrisation des concepts dans le domaine des maladies infectieuses. *Bulletin de la Société française de Mycologie* 19: 265-269.
- Grecias, P. and J. P. Migeon (1989). *Chimie; cours et tests d'application*. Editions "Technique et documentation (Lavoisier)", Paris.
- Pascaud, C. (1989). *Particules élémentaires*. Encyclopaedia universalis, Paris.
- Thom, R. (1975). *Structural stability and morphogenesis*. Benjamin-Addison Wesley, New-York.
- Thom, R. (1980). *Modèles mathématiques de la morphogénèse*. Christian Bourgois éditeur, Paris.
- Thom, R. (1986). Le problème des ontologies régionales en sciences. *Philosophie et culture*, actes du XVIIe congrès mondial de philosophie. Tome 1, pp. 195-204, Editions Montmorency, Montréal. Reproduced in [11].
- Thom, R. (1988). *Esquisse d'une sémiophysique*. Interéditions, Paris.
- Thom, R. (1990). *Apologie du logos*, Hachette, Paris.