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EVOLUTIVE STRATEGIES OF COLONIAL ANIMALS

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In the animal world, and not only, formation of colonies represents an evolutive strategy.

Association of several individuals and the formations of colonies, as based on the physical link among partners, leads to the manifestation of some morpho-functional modifications that grant to the whole structure thus formed superior qualities, and a well-established integrality.

The individuals' differentiation gets highly extended, so that some them seem to be organs of the whole, while the colony acquires the aspect and characteristics of a metazoon.

Which are the ways through which the formation of some highly established and functional colonies may be obtained? In the following, the author will suggest some possible explanations.

Introduction

The term of colony may have different meanings – as depending on the group of organisms under consideration. The members of a colony may be physically united (as is the case of Sponges, Coelenterates, Briozoa, Urochordata), or they may be differentiated in primitive and sterile castes or castes possessing both characteristics (e.g., ants, bees, white ants).

The colony may be formed of similar individuals, which live independent lives, although they are connected among them (*Codonosiga botrytis, Codonocalsium umbelatum*), of similar individuals (homonomous colony) which communicate among them through the digestive tube (hydrozoon coelentera such as: *Obelia dichotoma, Eudendrium ramosum*), or of morphofunctionally-differentiated individuals (heteronomous colony), which communicate among them and perform specific functions, absolutely necessary for the whole entity (Siphonophora, Briozoa etc.).

The colony is represented by a society formed of individuals which, from a certain level of morphofunctional organization on, may accomplish the functions of a well-organized and individualized organism or supraorganism. What is the *Cristatella mucedo*, an individual or a community?

What is, instead, the sinophoron *Physalia physalis*? In both cases, the colony is spatially well-delimitated, acting as a functional whole, some of its individuals acting as true organs. Why are we then talking of colony and not of individuals? Because the individuals are so much differentiated that, at a certain moment, it is difficult to say

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whether they are only individuals playing a certain role within the whole, or they are well-differentiated organs with precise functions in the system.

The individuals' morpho-functional differentiation within a colony seems to be a highly organized strategy of the colonial forms.

Is this rule characteristic also to the colonies in which the individuals are not morphologically connected among them? According to the observations of **Durkheim** and **Wheeler**, the society represents a supraorganism which evolves towards an ever increasing complexity, by means of differentiation and integration processes.

Consequently, within a society, two apparently contradictory principles seem to act, namely: differentiation and integration. Differentiation can be only achieved being actuated by integration. Any morpho-functional differentiation occurs only on condition that its main effect is assembly's integration. Differentiation is produced under a perfect and unitary control. Similary with the fact that differentiation is performed exclusively to the interest of integration, and of a higher interdependence among the compounding parts, integration cannot be attained and cannot become dominant in the absence of a multiple and intense differentiation.

When integration attained its maximum point, the term considered is no longer that of colony, but of individual.

In the colonies in which the individuals are physically connected among them, differentiation goes even farther, up to the point in which some individuals seem to be the perfectly functioning organs of a whole (which is a superorganism). The question may be, nevertheless, put in a different manner, if considering the colonies in which some of its individuals are not physically connected among them, namely: does not the attainment of integration necessitates the morphofunctional differentiation of some individuals, remainders of other organs' existence? It should be like this. This might be so if some castes characteristics to the social insects (ants, bees, white ants) act simply as organs performing certain functions.

The caste represents a group of individuals within the society, which plays one or several roles. Sometimes, the group forming a cast is not only playing a part, but it may differentiate itself by a peculiar morphological conformation.

In a society of insects, the phenomenon known as polyetism may be met. The term of polyetism defines a certain labour division within the society. The different activities may be executed by two individuals – which differ among them only as to their age. It may also happen that some workers should return to performing some of their previous roles – if this is a "must" of the society in a certain moment of time. Such a case may be considered as age polyetism.

Nevertheless, in such cases, too, the individuals' functional differentiation plays the same part as in the morphologically integrated colonies; this refers to the realization of certain functions. Once known that the functions of a metazoon are fulfilled by certain organs, in such case, the individuals differentiated into castes or in a well-defined polyetism behave as organs.

The evolutive strategy seems to be similar.

Deciphering of the way in which these morpho-functional differentiations occur, and of the meaning of such evolutive strategy is an absolutely fascinating research.

Evolutive strategies in colonial animals

The formation of coelenterata colonies is well-known. The authors' interest is to find out why the option towards complex colonies' formation was preferred to that of the organization of individuals with an ever increasing complex structure – which would mean an morpho-physiological progress. It appears that the formation of colonies represented quite an important way among the other evolutive strategies.

How are the colonies formed *Hidra viridis* is a solitary polyp. Even if it multiplies through budding, the polyps-sons get detached and live idependently. Multiplying through sexed ways, the egg-cell will contain all hereditary information necessary for the formation of a new individual. The same information is acquired by the individuals formed through budding. They, too, form ovules and spermatozoa.

Nevertheless, in certain hydrozoa species, the polyps formed through budding are no longer separated; instead, they remain attached to their mother, thus forming a colony. The colony is simple, homonomous, its individuals having a common gastric cavity. It may be either of momopodial-or simplodial-type, or it forms a lawn of individuals, connected through stolons. In some species, the individuals of the colony are seen as suffering morpho-functional modification, which leads to the appearance of a heteronomous colony.

Something is happening here. The genetic information gets different from one individual to another. The colony represents an advantage, as food is assured to all individuals, even to those that were not able to catch it. Gradually, the individuals come to depend on one another, the colony gets established and is manifesting as a whole.

Thus, polyps' differentiation begin. The first ones to be differentiated are the gonozooids, which take over the function of sexed multiplication. Thus, the gastrozooids remain to assure exclusively the feeding function. Differentiation advances, individuals with protection functions being then formed. In this way, in *Hydractemia carnea*, dactylozooid (with functions of active defence) and acantozooids (with functions of passive defence) are formed.

Gonozooids having a rapid evolution, generate medusae which, besides the reproduction function, take over, too, the one of species' spreading. It is assumed that individuals' morpho-functional differentiation is controlled by certain genes – which means that some polyps' different structure is given by the existence of some different genes. What happened, then? Some different mutations – which make such differentiations possible – did appear? A normal polyp's transformation into a gonozooid and the evolution, from this point up to the formation of medusae with a much more complex structure than that of the polyp, involve necessarily some major genes. That is why, the following question arises: how did these genes appear? Did some successive mutations – subsequently leading to major transformations, up to the level of medusae –

take place? If a multiple of alele genes is involved, how could their canalized appearance be explained?

It is obvious that a whole set of genes act for a dactylozoon's formation, while others are involved in the differentiation of a gonozoon or a medusoon. These genes control the differentiated formation of such individuals. Sexed reproduction is realized through eggs. How do these genes reach the level of gonozoon? Were they from the beginning in the genetic information of the individual forming the colony (the oozoon)? It is quite improbable that the hereditary dowry characteristic for a population of individuals from a colony's structure is occurring, from the very beginning, in a latent state, and ready to action in certain evolutive moments. This would support the idea of performance. More probably, such genes should have appeared at certain moments, in the course of time. But when and where did they appear? In the genetic information of the metamorphosized individuals? Were the transformations possibly accumulated in time and the structures were gradually improved – or not? The transformation of some normal polyps into medusozoon is impressive, indeed.

If the genetic modifications are characteristic to each individual, how can be explained the fact that some of these types (gastrozoa, acantozoa, dactylozoa), although not participating to sexed reproduction, do transmit their genetic accumulation?

How did the information reach the gonozoa, in the sexual cells? We shall leave aside their vehiculation according to the ideas of **Darwin, K. Nägeli** or **A. Weismann**. Such a transfer between individuals is not possible. And yet, the informational accumulations seem to be stored in the zygote's genetic information, although they belong to the colony's hereditary dowry. Caution! The egg cell characteristic to a colonial species does not contain only the own hereditary information of an individual (as one might believe), but of the whole colony. Where can the egg cell accumulate all the information from? How is it possible that the genes of each type of metamorphosized individual reach the egg cell? Which is the difference between the genetic dowry characteristic to a species with a homonomous colony and of one with a heteronomous colony? The colony represents a society of individuals. They live together and depend on one another during their lifetime, forming an unitary whole, an entity, a colony. In these situations, does the egg belong to a certain individual or to the colony – i.e., to the society of individuals?

If a colony belongs to an endemic species, which would be represented – at a certain moment – only by that colony – no matter how large or small is it – would this mean that the egg is of the species? Wouldn't it belong to an individual? Such a perspective makes the confusion total. The species does not produce eggs, it does not multiply. It is only the individuals that multiply, it is they that form eggs, the species being maintained by individuals' reproduction.

In the form it happens, reproduction is performed by individuals, however it is written in the species' programme. All reproductive behaviours characteristic to a species belong to the individuals, yet they are dictated by the species' programmes, being recorded in the individuals' genetic information. In the reproduction performed by the specialized individuals of a colony, there occur a highly subtle element involved in the process of reproduction, an incredible evolutive strategy of the species. From the moment in which, in a colony, labour's division gets intensified, and some of the individuals give up species' reproduction – a function taken over by specialized individuals -, the latter ones are obliged to include in the sexual cells all genetic characteristic of the individuals that take part to the formation of the whole – i.e., of the colony. Gradually, the egg looses the role it has, of genetically transmitting the realization of a certain kind of individual, acquiring instead the function of transmitting the features to the whole entity. The egg of a colonial species becomes the exponent of the colony and not only of a single type of individuals, even if they are gonozoa. In such a situation, the colony appears as a true superorganism.

Such a situation may seem absurd. It only seems, however. The discussion is developed around the term of population as an organization level, thus attributing to it all the characteristics of an organizational level. However, we are not capable of understanding the whole it forms. Could we somehow imagine that, in solitary species, there might exist individuals having not registered in the genetic information all the species' characteristics? This is not possible – it would be naïve from one's part to accept such an idea. Consequently, in this situation, too, the egg contains not only the information belonging to an individual but, equally, of the whole species from which it comes. This is correct reasoning.

Nevertheless, how does the genetic information characteristic to acantozoa reach the level of the reproducing cells of the gonozoa?

Things are quite complicated, indeed. All cells belonging to the individuals from a colony's level come from the egg cell, in the same manner in which all cells of a human body come, also, from the egg cell. This means that the cells contain all the genetic information necessary for re-building the whole. As, in coelentera, the individuals', and the colony's regeneration capacity is extremely high, the whole colony may be re-built from any framgement of it. Consequently, the cells contain the same genetic information why, there, then occur – within a colony – so many and different forms of individuals? The genetic information is the same, yet it is not read in the same manner in all cells. Reading depends on a multitude of factors. Part of the genes are blocked in certain parts of the colony, at certain individuals, while in other individuals other genes are blocked, and others are operating. Which are the factors that induce a different reading? They may be possibly cells' position within the colony, the relations among cells, the environment's different influence, etc.

Individuals' association within a colony assumes their submission to the whole's superior programs. Such submission increases with colonial integrality's increasing. This is as if, in the genetic information, new and new programmes – executed by the compounding parts (i.e., by the individuals) are registered.

The programs are not common for all individuals, yet they address – in a differentiated manner – certain categories of individuals which, by obeying them, begin to be morphofunctionally differentiated.

In a heteronomous colony, the individuals are differentiated as a function of the whole entity's interests. Do the individuals themselves attempt at being modified?

Why some of them become gastrozoa, while others become acantozoa or gonozoa? Do they choose certain functions by themselves? Probably not, more likely these functions are imposed to them by the whole, being selected exclusively to the interest of the whole. There seem to exist rather imposed programmes, that should be executed. Depending on them, only certain genetic information – different from one category of individuals to another – are utilized.

The major transformations occurring within a colony are not probably provoked by equally major transformations of the gena type but, rather new relations among genes are established, as a function of the new programmes that come to be imposed. They seem to be required by an internal tendency of the whole (the colony) towards the accomplishment of certain functions.

Taking upon ourselves the risk of be viewed as **Lamarck** supporters, we should nevertheless consider this factor – i.e., the internal tendency of human beings towards progress.

The transformation of a colony's individuals is occurring neither randomly nor chaotically, instead it is imposed by precise necessities. Whose are these necessities, however?

By no means of the individuals – taken separatedly –, but of the whole. No matter how anachronical this would seem, one may grasp an internal "desire", i.e. some interests of the whole.

The evolutive strategy of the colonial forms is based on the individuals' morpho-functional modifications, which makes them capable of performing certain functions. The differentiation may go so far that, at a certain moment of such process, nothing of the initial pattern is any longer recognizable.

How are these morpho-functional differentiations taking place?

In the beginning, all the individuals in a colony are similar. The gastrozoa perform the feeding function. They should catch the prey much easier and deposit it better for digestion in better conditions.

They may become bigger and stronger. Their tentacles are larger and their gastric cavity more spacious. They might possibly be supported by neighbouring individuals, which are also gastrozoa. They may group together, 2-3 or more, in a single place, yet a more substantial helps for getting the prey is felt as necessary. This would be much more simple to realize, and also over a much more extended territory, whether gastrozoa have some catching filaments with powerful cnydoblaste batteries. Could this possibly be a solution? If so, then it might be put in practice.

How? Through the transformation of some polyps into catching filaments. Well, but the distance is too large, and the transformations much too ample. Yet, nothing is impossible. A model, a pattern should be found out – applicable in all possible cases, in all kinds of similar colonies. Where from could such a pretention hade started? Probably from the colony's interest – the interest of the whole. So, what? Would this mean that some canalized mutations of the genes, leading to the appearance of individuals with such a type of organization, and capable of performing this necessary function, are to follow? The assumption is so naïve that it deserves nothing but immediate abandon. Then, such a transformation, which was seen as highly real, had only randomly occurred, without a command or at least a wish from the part of the whole? This solution is even more naïve than the preceeding one. The modification was the result of a necessity, and was developed as a function of the whole's possibilities. One should belive that the internal tendency of the whole had been manifested first, followed by the implementation of a certain program, adequate to such transformations.

After such implementation, the program will be finalized by means of the interrelations functioning among genes, as well as by various genetic modifications. Everything seems to depend on the "architect" genes that read and process the genetic programs.

The strategy of colonial systems seems to be similar to the strategy of metazoa's constitution, through a similar association of numerous individuals which are, however, unicellular. Labour's division within the whole permits the shifting towards organs' formation. The manner in which they appear is, to a considerable extent, different, however, essentially, they seem to represent the same organizational scheme.

A colony's complexity increases with the morpho-functional differentiation of the compounding individuals. At the same time, its integrality increases, too, so that the question arises whether a colony or a well-established individual is involved. What is *Physalia physalis* or *Velella spirans*? Are they colonies? Their body is so unitary, the individuals behave as well-individualized and organized organs so that it seems hardly probable that they actually are different individuals belonging to a colony.

Even in the case of *Halistemma pictum*, which is a primitive formation, the individuals are highly differentiated, forming an unity from the colonies. At their upper side, there occurs the pneumatophore (the syphonozoon) which performs the colony's vertical movement. The pneumatophore possesses gasogenous genes, which assure vesicle's filling. There follows the series of nectozoa, which resemble the medusae, assuring colony's vertical movement through propulsion mechanisms. On the stolon one may find series of individuals grouped in formations named chormidiae. A chormidia is formed of a phylozoon, which has the aspect of a bractea that protects the respective individuals formation. In each chormidia, one may find highly developed gastrozoa, linked to the catching tentacles, provided with strong nematocyste batteries.

The catching tentacles, which capture and paralyse the prey, may playing a protection role. Some of the individuals – named paplones – have the aspect of a sack. From paplones and gastrozoa, the long, catching tentacles are formed. The gonozoa, well developed, too, may have the shape of a sack (with the primitive forms), or of a medusoid gene – in the more evolved ones. The batteries of individuals, i.e., the chormidiae, are repeating along a stolon, which is penetrated by a gastric cavity that assures the connections among all individuals.

The stolon and all the chormidiae form the so called chormus – or the colony's body. The chormidiae are well-organized, functional, even independent in some species -

a case in which they live alone (being thus called eudoxiae). The colony is characterized by a continuous growth.

The new chormidiae are formed in the vicinity of the pneumatophores, the old ones occurring at the opposite end. The situation is comparable to the formation of proglottes in the case of tape worms. That is why, the detachment of some chormidae is not surprising. *Halistemma pictum* is a primitive species, in which the chormidae are arranged linearly. In the evolved forms - such as *Stephalia coron, Physalia physalis, Velella spiralis* –, the chormidae are arranged concentrically under the nectazoa.

The colony's behaviour is quite complex. The zoozoa, perfectly integrated within the whole's functions, behave as if they were the organs of an unique organism. Coordination of the individuals' activity is performed by means of nervous formations. Each metazoa has its own nervous system, which coordinates the contractions, being nevertheless connected to the rest of the colony again through nervous formations, so that they may respond to any signal launched by the colony's individuals. The gastrozoa may develop independent activities of prey's catching, although, frequently, there are several individuals that take part in the capture of a bigger prey. The paplones seem to be some auxiliary digestive organs, with the function of pumping the food along the stolon.

Quite interesting is the fact that the whole colony starts from an egg cell. The whole genetic information is to be found in the egg cell, from which the haired larva (the planule) is born. The ciliated larva puts the basis of the whole colony. Its ectodermis gets thickened and start to generate the buds of the nectozoa and of the pneumatophores, then of the other categories of individuals. A certain area remains functional, like a meristeme, generating new chormidia series. In this way, the so-called astogeny – i.e., colony's ontogenesis – occurs. The egg cell is the carrier of the whole genetic information necessary to the colony, no matter how complicated is it. That is, the egg cell carries the information of the whole society of individuals.

Along the evolution of the colonial forms, from the homo- up to the heteronomous ones, characterized by a complex structure, one may grasp the increasingly complicated evolution of the genetic material deposited in the egg cell. The egg is not of an individual, as we usually consider, yet it is of the colony's. The genetic material should register all individual differentiation, all new morpho-functional accumulations of the whole.

The colony represents a form of shifting toward pluricellular individuals. The cells that get associated in colonies should include this association in their genetic programme. Even if the cells are morpho-functionally differentiating, they have in their genetic information the program of the whole (i.e., of the colony). In the case in which the differentiation of structures within the colony is so extended that some of the individuals gave up their reproduction function, then it is compulsory for the individuals taking over such functions to register the whole genetic information of the colony. Such a principle is perfectly valid, too, for the structure and functionality of the solitary metazoon organisms.

In this way, one may understand the individuals' gathering within syphonophorous or within other heteronomous colonies. Assemblage is so perfect that some of the individuals seem to represent organs of the whole, functioning as a well-individualized whole.

Having all these in view, one may assert, without erring too much, that, in the case of syphonophores, the body is formed of organs represented by individual organisms. In the case of metazoa, the organs are formed at the expense of the embryonary foils. In the heteronomous colonial forms, the so-called organs are forming in different ways, although the final function is the same. One should therefore understand from here that the need of organs becomes a necessity for the accomplishment of the morpho-physiological progress. This cannot be achieved without labour division, without the intervention of some specialized structures. As a matter of fact, it seems that the manner in which these organs are forming is not important. In the case of coelentera, two ways through which the morphofunctional progress occurs may be differentiated. Polyp's evolution may be followed in the coelentera series. If, in *Hydrozoa*, the polyp is simple, with an undivided gastric cavity, in *Scyphozoa* - in situations in which the biological cycle is present – the polyp's gastric cavity is divided into four cells, through four septae. In *Octocoralli*, the gastric cavity is divided into eight cells through eight septae. These septae have a complex structure, as follows: their edges have the so-called mesenteric filament, with hairy and glandular cells, the septae have muscles: transversal muscles, on the posterior side, which grant septa's narrowing and gastric cavity's enlargement, and a septal retracting muscle, on the ventral side, each with the role of folding the septa in longitudinal direction. At the basis of septae, the gonads are localized. The polyp's structure gets complicated, while the functions are separated, being localized in a special type of organs. In the polyp's oral part, a pharynx – on which the septae are inserted – is differentiated.

Inside, the pharynx is lined by an ectodermis. Liquids' circulation in a certain direction is assured by a hairy ditch, called syphonoglyphe. Its cillia form a water current that penetrates the interior of the gastric cavity, while the cillia from the rest of pharynx's epithelium intensify the water current that leaves the body.

The organs are well-individualized and perfectly functional for the requirements of such organisms. The tentacles are situated above the loculi, while the gastric cavity penetrates them up to the pinule. Septae have an endodermic origin, however the two dorsal septae's edges have long cilia on their longitudinal bands, which delimitate a ditch, evidencing, too, endoblaste cells. These bands are ectodermic, originating from the pharyngean ectodermis. The transversal and the longitudinal muscles are originarily formed at the expense of the endodermis. Gonades are, also, of endodermic origin.

In the case of *Hexacorallia*, polyp's structure is even more intricate, which may be explained by the high number of tentacles and septae that form the so-called cells and inter-cells. The number of septae is so high that it delimitates the digestive tube through mesenteric filaments (which evidence a quite complex structure). Gastric cavity is divided both by scleroseptae and – in the forms possessing a skeleton – sarcoseptae.

Here too, the tentacles are found above the cells, their number corresponding to the number of cells. With several species, the mesenteric filaments continue, in their inferior part, with a long and thin filament, rich in cnydoblaste cells, called aconitum. Such filaments, which are extremely mobile, are both attack and defense organs. They may be drawn out either through the buco-annal orifice or through some apertures that penetrate the body's wall, known as cinclydes, being quite similar to syphonofores tentacles or catching filaments.

Of interest here is not to discuss some structures, but to underline that polyps' morphophysiological progress involves differentiation of certain structures, which occur as a result of certain cells' and tissues' grouping and specialization. Where is this tendency of forming organs coming from? Is their structuring a necessity, indeed, when the organisms claim higher living standars? Which factors determine the individualization, intrication and specialization of certain organs? Is this, indeed, an internal requirement of the organism, of the species? If so, does this involve the immediate occurrence of canalized mutations, meant at assuring their production? Such question have been already asked. However, under discussion here are not the individuals subjected to metamorphoses, but some structures, specific to the organism, that suffer modifications canalized in a certain direction. It is as if some function should be performed, and modification or creation of new organs occurs. Should digestion be enlivened? This may be realized by gastric cavity's dividing into compartments. How? By the creation of septae. Are they not sufficient? Then, their number should be increased. Are they not perfectly functionall? Then, their structure may be complicated. Is the involvment of a single embryonic foil not sufficient? It does not matter, another one may participate, too, to structure's realization.

Does the organism need some additional protection structures? The solution is the presence of some filaments provided with nematocyste batteries. This is the probable pattern that may be applied. However, at whose expense is this formed?

Does it matter, any more? Important is that they are forming. The solution is similar to that applied for the realization of other organs.

The observation may be therefore made that polyps' structure has become extremely complex, involved here being the formation of organs and only some individuals' differentiation within a colony. In the case of heteronomous colonies, a certain intrication of the whole's structure is also occurring, yet the solution is different. The role of organs is taken over by some individuals. The filaments or the catching tentacles which support the gastrozoa in food's procuring are similar to antozoa's filaments, although they are formed in a different manner.

Such homologous organs are to be noticed in the animal world in other cases, too. Actually, do not dolphins' wings play the same role as the sharks' ones? The fact that their origin is different is not important. Essential is that they perform the same function, with the same efficiency.

The authors have therefore drew the attention on two different manners of increasing the organisms' morpho-physiological progress, within one and the same phylum. Which of them is more efficient? Probably, the one of the direct formation of organs, once it is so largely applied. This does not mean, nevertheless, that syphonophores of the *Physalia*, *Stephalia* or *Velella* type are not liable to improvement and adaptation to the mode of life and environment corresponding to their evolution level and, consequently, to their living requirements.

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