Organisms and their place in biology

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Summary: In this paper we review the concept of organism analysing the main ideas related to it in the context of present biological theories. The discussion is focused and developed according to four key issues: individuality, organisation, autonomy and reproduction. Once these basic connections are established, a spectrum of possible entities that fall under the label 'organism' is looked over, with special emphasis on limit or controversial cases. The aim is to see whether they all share a set of common features and, if they do, why it is so difficult to reach a consensus on the definition of the term. Finally, we try to release somehow the tension between those hierarchical schemes proposed to account for life as a global phenomenon and those approaches that take organisms as the central target of (theoretical) biology, suggesting a possible middle-ground solution open for further research.

I. Introduction

Until quite recently biology was a science of the organism, but current philosophical discussions may even deny the existence of entities that fall into this category. The notion of organism is problematic. It is not simply that, for some time now, some of the life sciences do not have individual organisms as their object of study; it is also that their research approach and findings seem to challenge the central place that this notion has intuitively been assigned in biological theories. Biology seems to be fragmented

into different life sciences[1] and each takes as its object of analysis a particular aspect of the global phenomenon of life on Earth, which is viewed as unique and wholly connected. Sometimes the focus is on processes less global and more specialised than the organism, for example in some developments of molecular biology and its derivatives (genetic engineering, developmental genetics, etc.), or of gene-centred evolutionary theory. Others, the focus is on more encompassing aspects that take into account entities at a higher level than the organism, for example in some parts of evolutionary biology or of ecology. As a consequence, the focus seems to have shifted away from the organism itself. However, it is questionable whether there can be a science of the living without an adequate understanding of that notion.

Hence, the proposal of this subject for discussion suggests an intention to vindicate the centrality and importance of the organism for our discipline. The radicalness of this vindication may vary, although in its most extreme form it would argue that it takes upon it a burden that cannot be reduced to or subsumed in other concepts. In this sense, it would be a primitive concept, one that cannot be derived from others. In any case, underlying the supposed need for vindication is the feeling that the concept plays too marginal a role in the development of the life sciences, and that this marginalisation is wrong.

The viability of reducing or subsuming the concept of organism can be studied in various ways. One way would be to look at the different possible levels that constitute the complex phenomenon of life as a whole, so that the role of the organism in relation to other categories depends on whether the phenomenology at that level can be reduced to others or not. This is an interesting thread to follow. Yet, in our opinion, the defence of the organism as a central concept should rely on: a) how the distinction between organism and mechanism, understood in the broadest possible sense, is conceived. In other words, a radical defence of an organism-centred biology seems to contain the presupposition that organisms are bounded and informed self-organising systems whose processes cannot be fully explained in mechanical terms (Rosen 1991, Weber 2000). This would mean that most of living phenomena must be understood in the context of an organisation endowed with a system closure. The extent to which this can be proved will indicate how far the notion of organism can be abandoned and concepts at other levels adopted to explain biological phenomena; and b) on how the organism expresses the idea of living beings as opposed to a global view of life, with a special emphasis on aspects like autonomy and the capacity of a system to create its own world of meanings.

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[1] We suggest here a difference between the apparent synonyms 'biology' and 'life sciences', the distinction being that the first is centred on the notion of the living being and the second on life as a global phenomenon. We do not assume that this difference is coherently followed in the literature, but we find it useful for our purposes.

The question is then whether the concept of organism belongs only to folk biology – that is to say, to the knowledge that describes the apparent structure of the living world for us human beings (Emmeche 2000) – or it is a primitive concept which biology or life sciences cannot jettison. It may be that the answer to this question is not an all-or-nothing one, that is to say, it may be possible to decide that there are senses and domains in which effective life science research can proceed at other conceptual levels, even while the centrality of the concept in ontological terms is retained.

In any case, the continuous progress of the life sciences over the last few decades makes it necessary to reassess, and possibly rearticulate, the idea of the organism in the light of our present knowledge and the general conception of life as a global phenomenon, i. e. as a complex and extensive organisation. This paper is an attempt to do so through the exploration of different theoretical developments and concepts to which the notion of organism is usually related, such as organisation, individuality, autonomy, reproduction, hierarchy and, of course, the concept of life itself.

We shall start with a discussion focusing on four different key issues and their corresponding perspectives on the organism. The idea is to introduce some basic theoretical tools that are apparently needed for an investigation into what an organism involves, and at the same time to provide different means to argue about its real relevance to contemporary biology. Then, we present a brief overview of different examples of organisms, covering not only those cases which are usually taken indubitably to be organisms, but also more controversial ones which are helpful to foreground problems (sometimes avoided, or not explicitly stated) that make a consensus definition difficult. This will lead us to suggest that, in the context of hierarchical theories of life, organisms do not fit adequately onto just one (standard) level. The fact that there are both unicellular and multicellular organisms (plus quite a few controversial cases of "in between" organisations with, at least, some common characteristics) seems to give this category an unusual thickness that any global hierarchical theory of biology should address.

II. Organism: individuality, organisation, autonomy, reproduction

The notion of organism is not simple. There is an intuitive grasp of the properties that our common sense takes as important about organisms, but this fails to accommodate many examples we can think of in real life. As Stelreny and Griffiths comment:

> (…) there is no single definition. Instead, "the organism" turns out to be a highly contestable notion. (…) If there is a common-sense view of the organism, it is the idea that organisms are complex, coadapted, and

physically integrated. They have differentiated parts. They are physically cohesive, with an inside and an outside. Since many metabolic processes depend on the existence of this inside/outside distinction, organisms are often equipped with homeostatic mechanisms to ensure that the inside remains stable despite variation outside. One major problem with this definition is that it fits plants badly. (1999, p. 173).

Our aim here is to elaborate on some of the questions that must be discussed by present day biology by examining various problems that the organism poses in terms of four main related concepts: individuality, organisation, autonomy, and reproduction. As we will see, these four questions are tightly entwined, but it is easier to analyse in detail some of the different discourses around the notion of organism if we separate them.

A. Individuality

Organisms are the most salient example of particular individuals[2] in the living realm, and this individual aspect has played an important role in evolutionary biology. For instance, what some now call the 'received view' (see, e. g., Stelreny & Griffiths (1999)) is centred on the notion of organism as a non-problematic kind of individual. According to this view, the primacy of the organism in biology derives from a population conception (Mayr 1985) which claims that generalisations in biology have a different logical structure than those made in other domains. Instead of identical or similar copies of a given type, individual organisms constitute populations of unique members linked by a biological relation. The concept of a population of related individuals is different from the notion of a class and its members: whereas individuals are spatiotemporally bounded and unique, members of a class are picked because they possess certain common properties. The internal variation of a given population is produced by several means (mutation, recombination, etc.) and it is modulated by differential reproduction and other evolutionary forces. The assumption is that organisms – unlike other categories – are or tend to be individuals, in the sense that they are unique, not only genetically speaking but also as a result of their particular history of interactions.

Things change for this view if the notion of individual is further challenged. In evolutionary terms a change in a population must be considered in two steps: one, the generation of genetic variation and, two, the ordering of that variation by selection. Thus, the process of evolution requires two kinds of categories: one of entities that are copied (with variations) and inherited, and another of those which interact with the environment

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[2] Particularity and individuality are distinguished here. What makes an object particular is its spacetime localisation and material realisation, whereas the individuality of living beings entails a concept of uniqueness in terms of biological information and ontogenetic histories.

and are evaluated for viability, degree of adaptation, or fecundity. The received view considers that only organisms interact with the environment, thus selection will only pick or discard whole organisms. Variation may be studied in terms of individual genes (as in population genetics) but, in that perspective, studies considering isolated genes are only approximations to the real process. Others consider that the source of variation should be sought in whole genotypes, and not isolated genes (Lewontin 1992). However, the elucidation of the exact nature of the entities that accomplish these two roles in evolution has proved to be difficult, and many different interpretations of the empirical entities serving one or the other function have appeared in the literature.

The problem seemed to be solved with the proposal of a conceptual distinction between the two roles. Although primarily conceptual, it was a distinction meant to enable later empirical identification of entities having the respective roles. This distinction was made in two different fashions, relating to the ways in which the centrality of the organism was being challenged by the new approaches.

One, the gene-centred view (Dawkins 1976), takes the perspective that the relevant units by which the required variability of evolution appears are not organisms (or genotypes), but single genes. Thus, Dawkins coined the terms 'replicator' and 'vehicle' to refer to the two categories, considering that the only replicators are genes and the remaining biological phenomena are vehicles. His main reason for this is that, unlike asexually reproducing unicellular organisms, where the replicator can be the whole genome, in sexual organisms in which reproduction occurs through meiosis, replicators are single genes capable of competing to enhance their own replication. Vehicles, on their own terms, are not confined to the organism level either, because in his view, the determining capacities of genes reach much further than the construction of organisms (or phenotypes). They may even influence the production of many kinds of environmental constructions that are, again in his opinion, controlled by genes and will ultimately have an effect on their own selection. This is the notion of the *extended phenotype* (Dawkins 1982).

The dichotomy between replicators and vehicles was, in turn, challenged by Hull (1981), who considered that this conceptualisation failed to grasp the real importance of the two processes involved, because it made the entities on which selection acts (i. e. vehicles) the direct consequence of genes. Instead, he proposed to analyse biological phenomenology by considering the two kinds of categories in their own terms. These categories were called 'replicators' and 'interactors'. A replicator is "an entity that passes on its structure directly in replication" whereas an interactor is "an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential" (Hull 1980, p. 318). This new distinction confers on interactors a biological status distinct from that of

genes, but not confined to the notion of organism. In fact, many researchers have accepted this conceptual distinction and considered that different interactors can be identified on different scales or levels in biology. Whereas the first distinction places genes at the centre of all phenomenology, the second opens the scene to a possible hierarchical vision of individuals, in which we may distinguish both replicators (not every inheritance is genetic in Dawkins' sense) and interactors (different cohesive individuals) at various levels.

The advantage of a hierarchical view is that it makes it possible and acceptable to use different levels in considering the evolutionary processes. Some will insist on genes as the actual units of selection (Dawkins 1976), others will favour cells as such (Buss 1987), whereas others may think that 'group selection' has more importance than is generally acknowledged (Sober & Wilson 1998) or even that the really significant evolutionary changes take place at the level of species (Stanley 1979). We shall consider this problem again in the final section.

In any case, a global and historical picture of the nature of life has as an important conceptual consequence: the idea that individuals in biology are not fundamental, but emergent in an evolutionary process. Thus, even the concept of an organism, stemming from our common-sense notion of a multicellular metazoan, should be taken as a derived notion that has evolved. Although the organism could be understood as a minimal or basic unit of selection in intuitive terms, it has only reached that position as the result of an evolution towards a kind of cohesive dynamic system able to maintain a set of potentially complex functional interactions with the environment.

B. Organisation

We also have a strong intuition of an organism as an organised entity in which parts contribute to the realisation of the whole. However, organisms are at the same time entities in which it is not easy to divide the whole into neat parts so that their respective contribution can be exactly allocated (Wimsatt 1974). This problem has not always been acknowledged.

This can be readily accepted if we contrast the different ways of comparing an organism with a watch according to the Kantian and the Darwinian traditions respectively (Etxeberria 2000). For the Darwinian tradition this comparison poses the problem of the "argument from design" (developed, among others, by Aquinas, Hume and Paley). Paley said that if in crossing a heath one finds a watch, one would not think that it had lain there for ever (like a stone), but would infer that the watch must have had a maker: "Arrangement, disposition of parts, subserviency of means to an end, relation of instruments to a use, imply the presence of intelligence and mind" (Paley, in Ruse 1998, p. 38). In the same way, the design of organisms leads

us to accept the existence of a creator: "every manifestation of design which existed in the watch, exists in the works of nature, with the difference on the side of nature of being greater and more, and that in a degree that exceeds computation" (idem, p. 39). When the Darwinian tradition responds to this argument, a natural explanation of design is produced that requires no divine intervention – the principle of natural selection – but it permits a likening of the watch to the organism, perhaps accepting it as a good analogy. Kant had already used the same comparison in the critique of judgement, but in a rather different way. He noticed a fundamental difference between the two: whereas the watch is formed by fixed components, fabricated beforehand and later assembled, in the organism the parts are formed for and from the others, some parts producing the others. Kant accepts an internal teleology in the living system. Many authors (for example, Mayr) have said that the later development of the theory of evolution corrects the Kantian summon to teleology and makes it possible to explain this in another way. This may be true, but Kant points to a problem that the Darwinian tradition has not really addressed: the relation among the parts to form an organisation. In fact, for the Darwinian tradition the identification of watch and organism is not problematic, whereas the Kantian tradition feels that a distinction must be made.

This distinction implies that there is a difference between explaining function as a derivative of organisation, and as a derivative of adaptation (either in the historical or ahistorical way) as is usual in evolutionary biology. It also reveals another important issue: the difficulty of understanding the evolution of organisations. Evolution and organisation are difficult perspectives to bring together. This is probably the reason why important researchers who have worked on the problem of biological organisation, like Varela and Rosen, have somehow left the problem of evolution aside as a secondary issue[3].

We may say that defining the components of an organism requires referral to the role they play in its maintenance or its functioning and, vice versa, an organism cannot be fully understood except in terms of its main constituents and the processes they go through. In other words, an organism im-

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[3] Rosen, for example says: "We cannot answer the question (…) 'Why is a machine alive'? with the answer 'Because its ancestors were alive'. Pedigrees, lineages, genealogies and the like, are quite irrelevant to the basic question. Ever more insistently over the past century, and never more so than today, we hear the argument that biology *is* evolution; that living systems instantiate evolutionary processes rather than life; and ironically, that these processes are devoid of entailment, immune to natural law, and hence outside of science completely. To me it is easy to conceive of life, and hence biology, without evolution." (Rosen 1991, pp. 254–55). A similar feeling may be found in Varela (1979): "I maintain that evolutionary thought, through its emphasis on diversity, reproduction, and the species in order to explain the dynamics of change, has obscured the necessity of looking at the autonomous nature of living untis for the understanding of biological phenomenology. Also I think that the maintenance of identity and the invariance of defining relations in the living unities are at the base of all possible ontogenic and evolutionary transformation in biological systems" (p. 5).

plies a type of material organisation in which 'parts' and 'whole' are inter-dependent, maintaining a rather intricate dynamic relationship. The parts relate to the whole in functional terms; that is to say, the processes by which components are produced and interact are precisely those required for the constitution and maintenance of the organisation they integrate.

From this point of view the difference between a machine[4] (think of the previous example of the watch, for instance) and an organism is clear. In the case of the machine, it could also be said that one needs to know the role each of the parts plays in order to understand the functioning of the whole system; and, conversely, that each part gains something – some dynamic property – when the whole begins to work. However, the system can be decomposed, in the sense that the parts not only pre-exist but have their own identities regardless of whether they are integrating the whole or not. By contrast, in an organism, action (i. e. the actual dynamic process) brings about identity (i. e. the constitution of both parts and whole) in a fundamental way. And this is precisely why it is not a decomposable system.[5]

Both machines and organisms can be thought as systems whose behaviour is a consequence of the action of constraints on a dynamics otherwise ruled by physical laws (Polanyi 1968), but the nature of those constraints and the way they are integrated is quite different in each case. In a machine, the constraints are ultimately externally generated, whereas in an organism they are self-generated. This point is linked to the previous one, since mechanisms can be decomposed only if the dynamic organisation of the system does not play a causal role in the generation of the constraints that actually make it possible. In organisms, there is a recursive generation of constraints in which the organisation of the system is fully involved, which precludes any form of decomposability.

As a result, even if there are systems whose dynamics can be studied through partial analyses of the mechanisms that rule it, it is quite clear that organisms do not belong to this kind of system, since the complexity of their underlying organisation does not allow them to do so. In the last decade of the twentieth century, the discipline of artificial life (particularly referring here to computational AL) has provided new means and a complementary empirical perspective to understand this problem. The AL approach is essentially reductionist (in the sense of 'bottom-up'), and focuses on the identification, separation and modelling of relations between a bio-

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[4] We are aware that the terms 'machine' and 'mechanism' have been used in very different fields and also with diverse meanings. In biology, one of the most important uses of those concepts relate them to the issue of characterising adequately basic biological organisation, and thus their connection with the actual concept of organism. For more on this question see Rosen (1991).

[5] The total dynamic process that an organism consists in shows a greater degree of invariance or stability than the individual component parts, which undergo a continuous turnover. This is why globally there seems to be a simplification of the *partially* very complex dynamics.

logical entity and its basic components (usually taken as fundamentals of the model). Even if the biological plausibility of this approach may be questioned, the difficulties found and the effort required to model different aspects of biological organisations could be an interesting indication of their underlying complexity. In this sense, it seems quite clear that the main success and contributions of AL have taken place either at low level dynamics (e.g., hypercycles) or in higher ones (e.g., populations)[6], whereas the level of the organism remains a major challenge despite the efforts of such competent people as Fontana *et al.* (1995) or McMullin & Varela (1997). So results in this area of research may serve also to support somehow the idea that organisms show a higher degree of irreducibility than appears at other scales, such as the molecular or ecological level.

Consequently, the concept of the organism would be a fundamental, a unitary process in the phenomenological domain of biology, irreducible to physicochemical (or even computational) descriptions. However, this basic construct has further specific characteristics as such a unit, distinguishing it from other types of – subsequently developed – biological organisations, like colonies or societies. The latter may also constitute irreducible organisations but do not share the same features of identity as organisms (such as particular individuation and adaptive or reproductive properties, as we shall see).

C. Autonomy

The third characteristic of organisms is that they are somehow independent of the environment and are able to produce an internally defined identity, not governed by the processes of the environment (Varela 1979, Lewontin 1983). This property is generally explained as a consequence of an organisational closure of the system. Some of the self-generated components of the system have autonomously become its actual boundaries (or physical border), assuming the functional role of channelling the interaction with the environment, something which is absolutely necessary for the self-maintenance of that kind of system, far from thermodynamic equilibrium and endowed with an inherent dissipative nature.

An organism requires a very special type of cohesion between its constituents. The components of an organism are subject to tight, close-fitting, spatial constraints, even if such constraints are not at all like the rigid ones that keep a solid block together, for instance. In biological systems, the most basic, self-generated, cohesive constraint is the actual physical boundary of the system. In unicellular organisms this is quite obviously the membrane. In the multicellular case the physical boundary is consti-

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[6] And in particular, addressing evolutionary issues (i.e. dynamics in the sense of 'change through replication with variation in a population of components under some selective pressure').

tuted by a set (of one or more types) of differentiated cells that will keep the others together, establishing what is – in a first and basic sense – the "inside" and "outside" of the system, even if this may be a less clear-cut distinction at a certain level of complexity.

In order to be able to explain these characteristics a suitable account should not start with the notion of replicating information, or any other semiotic concept, but with other theoretical elements that allow some kind of continuity between physics and biology to be conceived, i. e., that make possible, if not an explanation, at least some sort of grasp of how organisms may have originated in the early history of the Earth (or how they may have originated somewhere else and later managed to arrive here from space, if an external origin is proposed). Interestingly, in the context of origins the notion of self-organisation tends to have as much relevance as that of natural selection. Nevertheless, the conceptual tool required here must be stronger than self-organisation, since the latter applies both to living and non-living phenomena. The key lies in autonomy (Varela 1979, Ruiz-Mirazo & Moreno 1998).

An autonomous system constitutes a special form of self-organisation that contributes to its own maintenance through action in a variable environment. It is therefore possible to talk of autonomy when self-organising systems become agents able to maintain themselves through actions in a variable environment. The main difference between spontaneously formed dissipative structures and autonomous systems lies in the inside/outside relation. Whereas a substantial number of the constraints required in the first case are external to the system, in autonomous systems the constraints shaping metabolic processes (including the construction and maintenance of the physical boundary) are endogenous or internally created by the system. Thus, autonomy brings about the notion of a system that recursively constructs those constraints which constitute it, actively managing the exchange of matter and energy with its environment. The internal organisation of the system adaptively modulates itself depending on the changes in external conditions. And this implies local and selective control mechanisms that enable the agent to perform a specific action among a range of possibilities.

This is the basis of the relative independence of organisms with respect to their environment. The organism is an entity whose interactions with the environment are actively modulated so as to achieve a causal closure with the maintenance of the conditions under which the agent can retain those very interactions (Christensen & Hooker 1998). Thus, the organism is an autonomous system that internally produces some functional constraining actions on its environment, so as to ensure the maintenance of its internal organisation. As a consequence, organisms create their own world of meanings, what Uexküll (1982) called their 'umwelt'. An organism manages its interactions with the environment adaptively and functionally and,

in that way, the system itself (its identity) determines what is perceived as relevant for its maintenance (Ruiz-Mirazo & Moreno, forthcoming). Therefore, autonomy does not imply a confinement of functional actions or processes to the inside of the system; rather, it demands external functional activity as well. Accordingly, autonomy involves a notion of an individual that uses the environment for its benefit and performs many of the processes required for its survival outside its own boundaries.

D. (Genetic) reproduction

The idea of autonomy is important but perhaps not sufficient to grasp all that an organism involves. For instance, it does not provide a clear criterion to distinguish multicellular organisms from other types of collective organisation, like colonies or societies, which may also show autonomous behaviour. Besides, and more importantly, the long-term endurance of organisms – spread all over the surface of the Earth for thousands of million of years – cannot be explained just resorting to the notion of autonomy. Therefore, it seems that an additional property is needed to characterise an organism more closely, and the capacity for (genetic) reproduction – which appears in both uni- and multicellular living beings – would be a good candidate[7]. Here, we will try to outline different arguments for this, which requires distinguishing first between the concepts of reproduction and replication.

Generically, by reproduction we understand a process through which an organisation that constitutes an operational unit generates (or contributes to generating, as in the sexual case) a similar operational unit. It differs from replication in that no process of direct copying is in principle required. Szathmáry and Maynard Smith (1997) distinguish between 'replicators' and 'reproducers', and conjecture that a significant transition took place from one to the other when organisms arose out of a world of populations of molecules replicating by template. At the same time, they suggest a close relationship between the processes of reproduction and development in organisms.

From the point of view of autonomy, it should make a difference whether an agent is able to reproduce its way of organisation (i.e., produce an equivalent agent) or not. Although connected, this is somewhat different from the discussion about replicators–interactors in the previous section on individuality, where the focus was on the evolutionary perspective. The reproduction of an organisation constitutes a problem of its own. In present-day living beings, reproduction is coupled to the replication of molecular structures (genetic information), which is probably required for indefinite hereditary evolution (Szathmáry & Maynard Smith 1997), but we

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[7] For a more specific discussion on the question of reproduction and its importance in biological phenomena see, for instance, Moreno & Etxeberria (1992).

could imagine a situation in which there are autonomous agents without an integrated genetic machinery.

In this plausible (prebiotic) scenario, the process of reproduction of an individual autonomous organisation – like a protocell – would not be as sophisticated and reliable as it is today, but it would not be trivial, either. The idea of reproduction by progressive growth and subsequent division of the membrane may be regarded as simple, or physically necessary (and therefore "just an inevitable consequence") once a threshold volume is reached by the system. However, it is simple in so far as the idea of the organisation required to sustain such a system is rather simple, too. As the agents (the protocells) become progressively more complex, they need to develop mechanisms to control their reproduction. Otherwise the actual process of reproduction would not be feasible anymore, and, besides, a continuous transition from that prebiotic stage towards minimal living beings would be hard to imagine.

In fact, even in unicellular organisms as we know them at present, the role played by metabolic mechanisms (and thereafter by the ongoing interaction with the environment) in the cell division cycle should not be undermined. Reproduction is not just controlled through the genetic replication machinery of the cell but also through other mechanisms based on biochemical oscillatory processes[8].

The reliable and sophisticated way of reproduction (i.e., what we regard as 'genetic reproduction') of even the simplest living cells involves a strong entwining of the metabolic and the replicatory processes that its basic components undergo. This would be necessary for indefinite, open-ended, hereditary evolution (as we mentioned above), but also to ensure the long-term self-maintenance of entities with such a complex underlying organisation.

With multicellular living beings the situation is far more complex, since the basic constituents of the system are cells that already have a genetically instructed metabolism, expressed in different forms (corresponding to the different cell types). However, the capacity to reproduce – as a whole individual – is more forcefully needed in this context if we are to speak about organisms in a clear and meaningful way. In turn, this requires the interweaving of reproduction with a process of ontogenetic development.

In a multicellular organism all somatic cells must have the same (or a very similar) genotype. If they did not, the viability of the organism would be uncertain. This, at least in a fair approximation, defines the genotypic identity of the whole organism, even if the particular phenotypes of the cells differ (and also differ from the phenotypic identity of the whole organism). Reproduction in a multicellular organism takes place through a pro-

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[8] The relevance of these processes in cell division was actually highlighted by Rashevsky (1960) half a century ago.

cess of development that makes possible the generation of a similar new organism (with a genotypic identity that is somewhat different, unless it is a clone) from a single – fertilised – mother cell. This involves growth by continuous cell reproduction and subsequent processes of cell differentiation.

An interesting argument could follow from all this, allowing us to see why development always goes together with a process of individuation. Tight spatial constraints (and in particular the construction of a physical boundary or boundaries) would ensure that the genetic identity of the new organism is preserved (unless mutations occur), and therefore that the reproductive capacity of the old organism is realised. In the case of an aggregation of cells (think, for example, of a colony) where spatial constraints are looser, there would be a much higher probability that a cell from the surroundings, with a completely different genotype, could become part of the ensemble (and thus, nothing would guarantee that all cells came from the same "mother", and their chances of constituting an integrated functional entity would significantly decrease).

Therefore, the success of reproduction and development would be connected to an individuation process, to the actual construction of a physical boundary, which makes sure that all the cells of the new organism will share, roughly, their genetic identity[9]. In other words: development could be regarded as the process that allows the 'second order' integration of autonomous individuation and reproductive capabilities.

In sum, from this perspective, autonomy (encompassing both the notion of metabolism and of *agency*)[10] would be complemented by the capacity of reproducing (genetically) as an additional basic feature that characterises an organism and makes it distinct from other types of biological organisation.

III. Different realisations/manifestations of organisms

Now that these different perspectives have been rehearsed, in this section we will consider different kinds of entities that are commonly or exceptionally called organisms, and their characteristics.

The origin of life does not consist simply in the production of self-replicating molecules able to evolve by natural selection. Life must have originated as some kind of autonomous organisation that includes self-repro-

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[9] This new and important role for the boundary of the system calls into question whether multicellular organisms are just "autopoietic systems of second order" (Maturana & Varela 1984), since the issue of genetic reproduction is clearly involved here (whereas, in the unicellular case, we could envisage an autopoietic system with no genetic reproductive capabilities).
[10] The relevance of metabolism as a universal criterion for life has been recently addressed in Moreno & Ruiz-Mirazo (1999) or Boden (1999). With regard to the link between autonomy and agency see, for instance, Ruiz-Mirazo & Moreno (1998).

ductive capacities. Nevertheless, the evolution of life itself involves the production of new types of entities that enjoy new forms of organisation based on the previous ones. Thus, beginning with a characterisation of what we call minimal organisms (section A), new types of organisms can be distinguished which derive from the pre-existing ones in an evolutionary process that Maynard Smith and Szathmáry (1995) call "major transitions". Each of these major transitions is associated with the emergence of organisms with enhanced abilities to produce, maintain and transmit information cohesively, and also with the emergence of novel forms of selection resulting from the evolution of those new organisms (Brooks 2000).

Here our aim will be to characterise different types of organisms or living organisation but, rather than in terms of evolutionary transitions or in broad taxonomic categories, following the key concepts discussed in the previous section.

A. Minimal organisms

According to what we discussed in section II, an organism would primarily be a self-maintaining, autonomous and physically bounded entity. From that perspective, the question of determining the minimal organism is more related to the kind of properties that make a physically sustained and self-maintaining entity, than to capacities such as reliable reproduction or the ability to evolve (which presumably were acquired on the basis of pre-existing autonomous systems and probably only persist in so far as they continue to be part of – more complex – autonomous systems).

Following those lines, the basis of minimal organisms rests in the domain of component production dissipative systems, able to catalyse and regulate the synthesis of all the components required by the system network. Two basic processes characterise this kind of system: First, a thermodynamic process capable of partially compensating for the spontaneous degeneration of ordered energy states into disordered ones. In this sense, the maintenance of the system organisation requires the continuous production of work, i.e., the constraining of energy flows so that a dynamics is generated that reinforces those flows. Second, the constitution/production of a spatial boundary or separation between the system and the environment, that is to say, a membrane. Its role is not only to act as a global constraint on the enclosed processes, but also to keep a functional control on the exchange of matter and energy between system and environment.

Thus, the minimal notion of an organism involves a metabolism, as a chemical system enclosed in a selectively permeable membrane produced by the system itself and capable of self-maintenance. It is an operationally closed system that performs functional actions on its environment to maintain such far-from-equilibrium cohesion. Therefore, the individuation capacity of an organism is associated with the basic property of autonomy.

The question that still remains open is whether this is enough to speak about organisms (even in a minimal sense) or whether we need to resort to (genetic) reproduction because it is important to address also here the issue of evolvavility[11].

In fact, all the unicellular organisms that we know of have a genetic machinery. However, it is not easy to specify the original role of the genome for minimal autonomous systems like the ones just proposed (since existing organisms have endured a long evolutionary process). One of the problems we face is that, even though research in dissipative systems and origins of life has produced many models of the kind of proto-metabolic cellular systems we discussed earlier, the spontaneous origination of a simple autonomous system endowed with some sort of genetic apparatus never happens in the life with which we are familiar. Thus, there is much speculation about the minimal size and minimal functionality that a genetic machinery for such a minimal system must have (Lawrence 1999), but few clear conclusions.

In principle, a genetic machinery for systems reproducing by simple division (or cleavage) is required to ensure that the metabolic constraints producing the self-maintenance of the autonomous system are reliably transmitted to the "daughter" system. The details of the transmission are not difficult to explain: it is a process in which replicators copy themselves by base complementarity. The problem lies, of course, on how the relation between the replicating genes and the constraining components (presumably proteins) is established and transmitted. In any case, genes are sequences of nucleotides functionally related to a metabolism, and although the structural details of that relation are still obscure, we may imagine that the basic genes of minimal organisms would code for the proteins that regulate their own transcription and basic metabolic paths. Important issues such as the amount of connectivity required for such a minimal genome are not clear, but presumably in the beginning it must have constituted a system completely immersed in the metabolism itself and replicating as a whole[12]. This kind of minimal organism encompasses a dynamic identity (interactor), together with a replicator acting as record or memory of the system dynamics (Pattee 1969).

Therefore, the idea of minimal organism may be thought as the primary confluence between two different processes: metabolism and reproduction. In order to have an agent with open-ended evolutionary capacities, it

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[11] We discuss this problem within the framework of von Neumann's model of self-reproducing automata in Etxeberria & Ibáñez (1999).

[12] Originally reproduction is asexual, and there might not be such a strong necessity for distinguishing isolated genes (even if those who defend a strict correlation between genes and functional units – i. e., proteins – argue against this). The genome may then be conceived of as a global dynamic system, more directly entangled with the metabolism than we usually imagine for metazoans (probably in such a way that it makes less sense to distinguish portions of sequences as genes).

seems necessary that the organisation so formed is able to reproduce with inheritable variations. Hence, we could say that the first organism appears in the most elemental form of autonomous organisation with ability to reproduce, transmitting its organisation (with occasional changes) to the next generation.

B. Multicellular organisms

Although the idea of the minimal organism has been described so far with single-celled organisms in mind, it is more usual to think of multicellular entities as the first or more intuitive idea of organism. Today taxonomists consider that organisms are distributed into five kingdoms (Margulis & Schwartz 1998), with some organisms unicellular and others multicellular. The choice of a single-celled minimal organism as a starting point is partly justified by reasons of evolutionary precedence, and also because they constitute a great part of the biota. Although we do not intend to discuss here whether there is an increase in complexity in the transition form unicellular to multicellular organisms[13], it is of interest that multicellular organisms originate from single-celled ones and that in their constitution there is some loss of the freedom by which single cells ensemble to form a new type of unity. Thus, although the notion of autonomy applies intuitively to all organisms, this concept contains in one sense a paradox: multicellular autonomous organisms are possible only after single cells lose part of their autonomy. That is probably the reason why it is easier to propose theories of living organisation at levels that imply a transition from the inanimate to the living than at other levels, where the conditions are varied and what is emergent is not the property of being autonomous by itself (which must be acknowledged in some sense as pre-existent), but different forms of autonomy as aggregated organisations of systems capable of independent existence, at least in principle.

However, even the processes facilitating aggregation are not of a single kind. The types of dependence into which cells enter may be differently characterised: as a metabolic unity, as a genetically homogeneous unity, as a reproductive unity, etc. At the extreme is the idea, expressed by many researchers, that the world of bacteria is a single superorganism, whose individual component cells rely for their survival on ecological exchange of metabolites and on genetic exchange via plasmids and phages. This would imply a controversially high degree of horizontal genetic exchange among individuals, as apparently different lineages with little crossing between them can be distinguished for long periods of time.

In any case, the most common example of a multicellular organism (or at least the one that is closest to us) is linked to other processes that involve

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[13] Many people have recently opposed this "increase in complexity" vision of evolution. See, for example, Gould (1997) or McShea (1996).

cell differentiation (to produce different functions), usually starting from a single cell (reproductive bottleneck). Multicellular organisms with differentiated cells have evolved independently on at least three occasions to give animals, higher plants and fungi, conforming to different developmental schemes.

According to Buss (1987), a crucial step in the origin of multicellularity is the appearance of gastrulation, in which a hollow ball of cells is transformed into a multilayered structure and diverse patterns of cell differentiation. His study seeks the origins of multicellularity in the necessity to combine movement and reproduction in single cells. This derives from the observation that the cells of a metazoan can be either ciliated or prone to divide, but not both. The reason is that both undulipodia (cilia or flagella) and mitotic spindles require microtubule-organising centres, and thus either one or the other structures are possible in these cells, but not both. The gastrula would be the "solution" to this problem, where the cells on the surface remain ciliated and those of the interior lose their cilia so they can divide.

The reproduction of multicellular organisms is a complex problem and for most of the living taxa the germ/soma separation does not apply. Buss (1987) studied the evolutionary emergence of homogeneous multicellular organisms as a competition between cell lineages to become germ cells, taking the unit of selection to be at the level of the cell. In some organisms this evolution has produced homogeneity because germ cells are sequestered at very early stages of cell differentiation, but many other forms of reproduction exist in the living domain. The two strategies, reproduction and growth, seem to be matters of degree, rather than alternatives.

Cells in a multicellular organism lose their autonomy (through irreversible differentiation processes that make them apt to live only in a very specific environment, tightly surrounded by other cells) to serve a more global cause, that of an entire organism. Therefore, they depend on other cells, and ultimately on the ones that are part of the physical boundary, to obtain the material and energetic resources needed to carry out their own metabolism. As a result, the physical boundary of both uni- and multicellular organisms seems to play a similar role in the issue of channelling the interaction with the outside, although it is far more critical in the unicellular case where there are fewer intermediaries and the interaction with the environment is more direct. In the multicellular case the cohesive, interactive and protective role of the boundary may be taken up by other much more sophisticated mechanisms: for instance, in some phyla these tasks are facilitated by the emergence of the nervous and the immune systems, that provide further unity.

C. Aggregates, groups, superorganisms

If it is not possible to give a single definition of what an organism is, neither is it easy to distinguish the separate categories that conform to the notion of clusters or aggregates of organisms. Just as we could distinguish between minimal organisms with and without genome and with and without sexual exchange, multicellular organisms may or may not have bottleneck reproduction (as well as a clear germ-soma distinction) and may or may not show genetic homogeneity.

In this context the range of cases is very broad, and problematic examples are easily found. For instance, in the case of insect colonies, there is division of labour (similar to functional organisation), an apparent reproductive bottleneck (through a single individual), very close genetic content (due to haplo-diploidicity) and little independence of the individuals outside the whole organisation. Some people have called insect colonies superorganisms, but are they really equivalent to organisms?

These collective organisations do not have a physical boundary providing precise topological features or requirements (their size is quantified according to some other criterion, such as the number of individuals that belong to them). Colonies are spatial aggregates without a distinct functional boundary, composed of individual organisms that do not go through major changes in their particular constitution as individuals. As such, colonies have an organisational structure whose stability is maintained through the interactions among their members. A society, in turn, is a special kind of colony that involves, indeed, irreversible changes in the individual systems (always multicellular) constituting it. These changes are such that they do not allow those individual entities to enjoy an existence independent of the actual society.

Other interesting cases such as the Portuguese man of war (Gould 1987), or lichens, also challenge any unidimensional definition of organism. In these cases, as in the symbiotic and aggregative phenomena of many protoctists there exist types of cooperation among different entities that question any simplistic conception of individuality and appear to be calling for new theoretical developments in the ideas of unity and organisation.

Therefore, at this stage in evolution, multicellular organisms seem to be exploring the world of possible interactions and functional couplings (at times requiring internal changes that involve some loss of autonomy for the benefit of the group), in order to constitute stable supraorganismic organisations. The issue of whether these organisations can or cannot be regarded as superorganisms is a matter of debate, but we should not be surprised if that becomes the case in the future, when some new mechanism(s) of integration is(are) found and realised by nature (see Figure 1, final section).

IV. Life: genes, hierarchies, or bounded organisations?

So far we have reviewed and searched into the meaning of organism, exploring both its lower and upper bounds – from 'minimal' to 'super' organisms –. However, life is more than just a collection of organisms. As we said in the introduction, the life sciences have shown us that there are other entities which are relevant to explain various phenomena in the biological realm, and it is important to study the relationship of those entities to organisms and their respective status as significant biological categories. In order to do that, it is necessary to resort to some global, or at least more inclusive, framework which gathers together the distinct dynamics of things like genes, metabolites, cells, colonies of cells, multicellular organisms, populations, species, ecosystems, etc. This is not an easy problem to handle (much less to solve), but hierarchical theories appear to be the finest – if not the only suitable – way to tackle it.

The concept of hierarchy played an important theoretical role in biological thinking during the last century, although it has been used in different ways (Grene 1987). Hierarchical approaches that involve 'dual control' relationships between levels seem to have outshone other types of hierarchy with a less interactive vocation (like taxonomic, classification or simple scaling hierarchies). This move has been supported by the progressive realisation by theoretical biologists that cross-scale non-linear effects are indeed a characteristic feature of living organisation. As a result, nowadays it is generally accepted that the phenomenon of life involves a global and hierarchical organisation, which is maintained through interactive processes taking place on quite different spacetime scales.

Nevertheless, depending on the object of study and the type of interactions considered, different kinds of hierarchical schemes have been proposed. Since the development of molecular biology, the basic and minimal hierarchy regarded as necessary to understand biological phenomena involves the distinction between genotype and phenotype, i. e., the distinction between the level of genes on the one hand, and the level of organisms (or organismic features) on the other. Accordingly, the principles for the organisation of a biological system would have to be found in the interaction between at least these two levels. This approach has led to fruitful hierarchical schemes, such as in the work of Pattee (see, for example, Pattee (1973)), who defends the basis of the constitution of a living organism on the complementary relationship between what he later called the "dynamic" and "linguistic" modes (Pattee 1977).

However, present views tend to favour hierarchies with a more extensive series of levels[14], where transitive properties typically apply (for instance,

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[14] Possibly, one of the main reasons for this trend is the strength that the debate on units of selection has acquired in the last decades, which certainly promotes wider hierarchical conceptions of living phenomena.

the property that for any given level the ones immediately above and below tend to play the most relevant roles in all what concerns that particular level's dynamics). This, in turn, produces an idea of hierarchy as a sequence of levels (at least three), each of which is constituted by different entities/units/individuals (Eldredge & Salthe 1984). Accordingly, the interactions take place between individuals (at the same or some different level), rather than between *components* of an individual (e. g., an organism) that come together to build it up. Furthermore, the dichotomy between genetic (informational) and phenotypic (energetic/economic) features is extended to the whole hierarchy, which becomes a dual structure of two parallel but interrelated hierarchies (the "genealogical" and the "ecological", in Eldredge and Salthe's terms; see Table 1 below).

Table 1: (Taken from Eldredge & Salthe 1984)

Genealogical hierarchy	Ecological hierarchy
Codons	Enzymes
Genes	Cells
Organisms	Organisms
Demes	Populations
Species	Local ecosystems
Monophyletic taxa	Biotic regions
(Special case: all life)	Entire biosphere

This kind of attempt not only constitutes a remarkable effort to integrate two contending schools in biology (the "organisational" and the "reproductive" schools, so to speak), but also establishes a framework that combines without apparent conflict the independence (in that the organisation of levels and the reducibility relations may be considered separately in each of the parallel hierarchies), and interdependence (in so far as the interactions across levels of different hierarchies are essential to explain certain biological processes) of these two views. In addition, the explanatory value of such a conception is undoubted, since it establishes a precise taxonomic method with explicit assumptions about the relationships between classes of the same hierarchy.

In any case, a conceptual transition of this nature – i. e., towards a wider hierarchical scheme – involves quite an important change in the way in which life is understood, which is not always made explicit in the literature. Is life something that should be thought about in terms of the properties of (individual) living systems, even if some idea of hierarchy is fundamentally necessary to give an adequate account of them? Or is life, rather, a (global) hierarchical way of organisation involving lots of entities at different levels, where we tend to give more importance to living systems (to organisms) because each of us just happens to be one? In other words, what is the relative importance of the concepts 'organism' and 'hierarchy' for biological discourse?

For some people (and we could include here not only Pattee (1973), but also Varela (1979), Rosen (1991), and others) all the possible levels of organisation present in biological phenomenology are build on a fundamental construct: the organism. Accordingly, their primary goal is to explain the basic organisation of organisms, as compared to simpler physico-chemical systems. It is assumed that only when the basic organisation of living beings is elucidated can we begin to grasp how they interact and establish more complex (and further hierarchical) interrelation patterns. Alternatively, (e. g., Eldredge and Salthe's approach), the idea of hierarchy is used in a broader way, as an attempt to encompass the whole phenomenology of the biological realm; the notion of individuality implied in this second approach is weaker, and thus more general (i. e., can be extended to other biological 'entities' such as genes, species, ecosystems, etc.), with the result that the traditional importance given to the level of (individual) organisms is dissolved. Nevertheless, organisms tend to retain some special status in the latter hierarchical schemes as well[15]. So, what is it that makes organisms such a special biological category?

V. Final discussion: Is the organism a special category?

Are individuation processes that take place in the construction of an organism somehow of a unique nature? Are organisms special individuals in the biological hierarchy (or hierarchies) because they constitute the medium where evolutionary (selective-environmental) forces and self-organisational (internal) ones meet[16]? Are organisms the only type of individual that conjugates a functional and self-reproductive identity at the same time? What is then the significance of the organism for biology? These are some of the questions that need to be answered in order to grasp the deep meaning of the concept 'organism'.

A first reflection on this issue shows the difficulties involved. Even if we adopt a theoretical framework such as is offered by Eldredge and Salthe, it is quite clear that the organism cannot be conceived of as a mere contingent crossover point between the genealogical and ecological hierarchies. It seems to us that, compared to others, the level of organisms presents an atypical thickness, spreading over its uni- and multicellular expressions, and fusing the two hierarchies in a far more significant (and we could even say, constitutive) way than these authors propose (see Fig. 1 below). After all, if living beings such as bacteria and vertebrates, which are functionally and organisationally so different, are included under the label 'organism' it

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[15] In the case of Eldredge and Salthe's proposal, the organism is presented as the only level in common between the "genealogical" and "ecological" parallel hierarchies. This can be challenged, as we shall see next.

[16] An *active* medium, which becomes "the subject of its own evolution" (Lewontin 1983).
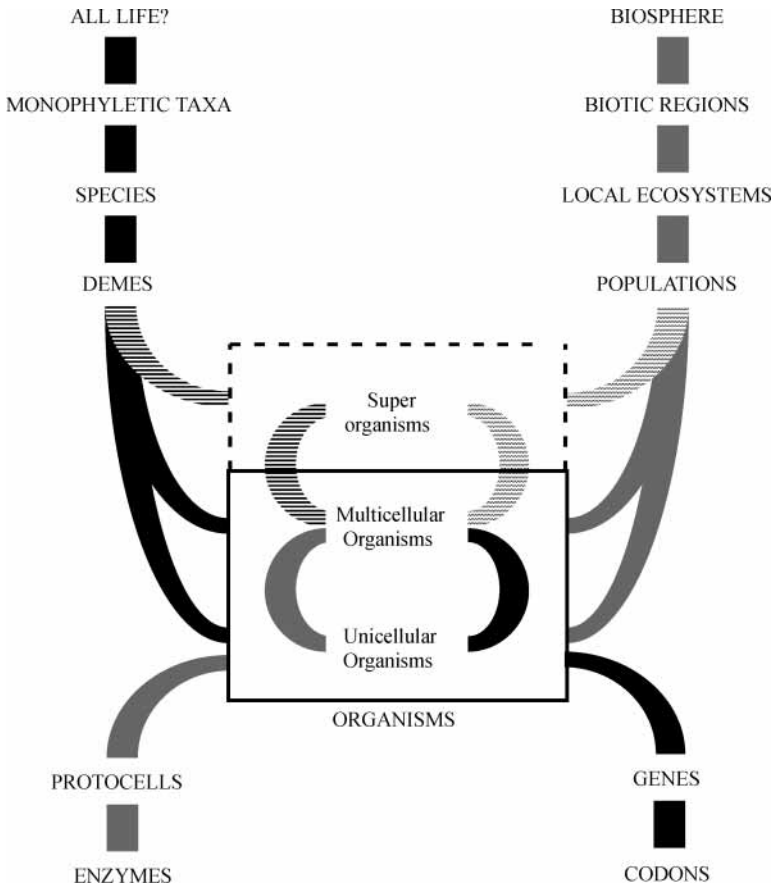
Fig. 1: This graph tries to show that the level of organisms cannot be just a crossing point between the "genealogical" (in grey) and "ecological" (here in black) hierarchies, presented in Table 1 before. A slight change in the previous category 'cells' (in favour of 'protocells') has been introduced for conceptual clarity, as well as the distinction between 'unicellular', 'multi-cellular' and (not so clear but possible, or still to be fully developed – thus the dotted lines –) 'super' organisms. The graph also suggests that the transition from uni- to multi- cellular systems (an estimated time period of about half the whole history of life on Earth) took place after both hierarchies had been already explored "upwards" by the former. Thus, the unfolding of the two complete hierarchies as we know them at present may be more tightly linked with this transition than usually acknowledged.

is because they share certain features that define them as units in both hierarchies. Therefore, a notion of organism that denotes a particular way of organisation and that remains irreducible to mechanistic approaches is required. But the notion must be specific enough to differentiate itself from other types of organisation, such as autocatalytic cycles, genetic sequences, or metabolons "below", and colonies, societies or ecosystems "above".

What then is the significance of the organism for biology? Our discussion has revealed that, although the notion of organism remains a key concept

to understand the living domain in our everyday life, it is not necessarily a theoretical tool that will act as a guideline for all the life sciences. In fact, not all of those disciplines need to be confined to the organism: over the last few decades they have produced different technoscientific tools to explore living phenomena as new types of mechanistic regularities. Some of them are useful for different purposes, such as the invention or discovery of new possibilities of intervention into nature (the generation of new medicines, alternative food resources, etc.). However, living beings as such are unavoidably systemic and should be studied in a theoretical context coherent with that. Even the development of nonsystemic techniques or products of a certain living kind (like those mentioned above) requires risk assessment and thorough evaluation of their potential and actual effects on organised biological entities.

In this sense the notion of organism constitutes some sort of primitive which cannot be reduced to separate mechanisms, and thus it shares many epistemological characteristics with other fundamental questions, such as that of consciousness, which are somehow opaque to a mechanistic type of knowledge.

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