

# Concept

## Individuals versus Individualities: A Darwinian Approach

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### Abstract

The idea that natural selection acts on many levels—and not only at the level of organisms or individual genes—is increasingly accepted among biologists. However, it is not easy to reconcile this idea with the strictly “individualistic” conception of the evolutionary process that has always characterized Darwinian thought. Moreover, the individuality of some forms of life is a vague concept and therefore controversial. This is the case of *Candidatus Magnetoglobus multicellularis*, whose discovery immediately inspired the following question: Does the concept of individuality have degrees? Alternatively, how far is this structure of prokaryotic cells from deserving to be called an organism? In this article, we propose a new conceptual scheme based on an idea of individuality that is not limited to organisms and that makes sense in terms of Darwinian evolution. In this conceptual scheme, selection at levels above that of the individual organism is interpreted as the evolutionary emergence of higher-level individuality. This proposal may serve as a basis on which to construct a promising hierarchical evolutionary theory.

### Keywords

compactness, centralization, development, differentiation, identity, independence, individuality, irreversibility, reproduction, unit of selection

Any real object divides the world into two parts—itsself and the rest of the universe. Both parts influence each other mutually through a boundary that is more or less defined, so that changes in one part induce changes in the other. Living systems in particular are characterized by their tendency to become independent from the uncertainty of their environment, which is equivalent to the perpetuation of a certain identity of their own. This leads to the following definition of biological individuality (cf. Wagensberg 2009): *A living individual is a part of the world with some identity that tends to become independent from the uncertainty of the rest of the world.*

A living system cannot isolate itself from the world to avoid extinction and maintain its identity independently from the caprices of the environment, as all isolated systems tend to thermodynamic equilibrium (i.e., death). To stay alive, a steady state must be maintained that is far from thermodynamic equilibrium. This is achieved by the exchange of matter, energy, and information.

The exchange of matter and energy between a living entity and its environment is a topic that is well described by equilibrium thermodynamics (Lurié and Wagensberg 1979). This exchange can be summarized by the balance of entropy:

$$\delta S = \delta_i S + \delta_e S, \quad (1)$$

where  $\delta S$  is the variation in the entropy of the biota,  $\delta_i S$  is the production of entropy that is dependent on the irreversible processes that occur within the system, and  $\delta_e S$  is the exchange of entropy between the living entity and its environment. The steady state corresponds to the necessary condition:

$$\delta_i S = -\delta_e S. \quad (2)$$

The exchange of information between the living entity and its environment is a topic that has been well described in the mathematical theory of information (Shannon 1948). If  $E$  represents a source of information called the environment and  $B$  is another source of information called the biota, we can write the following mathematical identity:

$$H(E) - H(E/B) = H(B) - H(B/E) = I(E, B), \quad (3)$$

where  $H(B)$  is the complexity of the living being,  $H(E)$  is the complexity of the biota,  $H(E/B)$  is the biota's ability to anticipate the uncertainty of its environment,  $H(B/E)$  is the sensitivity to change in the environment with respect to the complexity of the system, and  $I(E, B) = I(B, E)$  is the information transfer between the system and its environment. This equation can be challenged by incorporating the thermodynamic aspect described in Equation (1) and asking, in highly general terms, the fundamental question concerning a living entity (cf. Wagensberg 2000): *How can a living entity stay alive when the uncertainty of the environment increases?*

Various solutions are possible: increase the complexity of the system; reduce the uncertainty of the environment by means of mobility or technology (moving away from the environment or changing it); decrease the environmental impact; or changing one's own identity, i.e., changing the complexity of the system. This occurs, for example, when several individuals decide to join together to form a new individuality. What happens when a system is not adaptable enough to anticipate the unpredictable environment?

In this case, the living system should establish a steady state that is compatible with the new environmental uncertainty. It can only persist at the cost of sacrificing (at least some of) its former identity. In other words, to recover its independence from the uncertainty of the environment, the living system may have to adopt a new identity. In turn, this may lead to the emergence of higher-level individuality. We will now look at how this can be achieved.

### Supraorganismic Individualities

There are two main methods of evolutionary innovation: by *mutation* and by *association*. Any mutation with a phenotypic effect will lead to a new steady state. Innovations that arise in this way may thrive and propagate themselves, if favored by natural selection. The other way of creating new steady states, which we are going to discuss here, consists of combining two or more separate steady states into one. In other words, individuals join together to create a new individuality with a higher level of organization.

There are various ways of generating a new individuality that can adapt to new conditions of environmental uncertainty through the association of individuals whose separate survival is seriously compromised.

1. *Cloning*: One of the main sources of higher-level individuality is cell division leading to clonal cell aggregates. These can evolve to become complex multicellular organisms with their own individuality (Grosberg and Strathmann 2007). At the next highest level of organization, the same multicellular organisms can clone themselves to produce colonies of undifferentiated individuals (such as corals) or real superorganisms with morphologically and functionally differentiated parts (e.g., siphonophores) (Mackie et al. 1987).
2. *Symbiosis*: Another common source of higher-level individuality is symbiosis. Symbiotic associations may become irreversible, with complete interdependence between the symbionts, which are no longer viable separately. In this case, symbiotic fusion produces a new higher-level individuality (Margulis and Sagan 1997).
3. *Kinship*: The third source of higher-level individuality is kinship. Family groups can become highly structured and differentiated societies that function almost as superorganisms. This is the case in insect societies, in which a majority of sterile

individuals work for the reproduction of a minority of fertile individuals (Wilson 1971).

Unlike mutations, associations by means of cloning, symbiosis, or kinship lead to a rise in the hierarchical level of organization of living matter. Low-level individuals (associated individuals, whether they are cells or multicellular organisms) sacrifice some of their independence in exchange for belonging to a whole that is more independent from the uncertainty AQ2 of the environment than its members individually.

This does not present too many theoretical problems when the parts and the whole have 100% the same genetic identity, as is the case of cloned associations (which are formed by unicellular or multicellular organisms that are genotypically homogenous). Neither are there major problems in the case of symbiotic associations, as each of the symbionts tends to perpetuate its genes itself, in parallel to the other symbiont. However, sexual reproduction, which involves crosses and gene recombination, presents some problems with respect to the selection unit.

### Sexuality As a Generator of New Individuality

Classical Darwinism focuses on the individual on which natural selection acts. Individuals survive or die and leave more or fewer descendents depending on the adaptation of their physical and behavioral characteristics to their conditions and way of life. The individual is a unit of selection and/or a unit of evolution. The first means that some type of selection acts directly on the unit. The second implies that a certain identity is perpetuated.

Maintenance of identity could clearly be interpreted in many ways. However, we could state that, at the very least, it means that some properties do not change beyond a certain tolerance interval. With respect to Darwinian evolution, what is of interest is the perpetuation of genetic identity.

Unlike asexual organisms that reproduce by cloning themselves, sexual organisms lose their individual genotypic identity when they reproduce. Thus, the individuality on which selection in theory is exercised (the individual male or female) does not correspond with the identity that is perpetuated in the following generation. This has been seen as a paradox, as sex does not seem to provide any obvious adaptive benefit to the individual (Williams 1975; Maynard Smith 1978). By way of a solution, Williams (1966) and Dawkins (1989) proposed that the real unit of selection is not the individual organism but the gene. They considered that although selective pressures are exercised on organisms, in fact it is the genes that are selected, as they remain unchanged in the next generation.

If it were not for sex, gene selectionism would not represent a conceptual break with classical Darwinism. Asexual organisms produce clones of themselves, so the genetic identity of the individual (its genotype) is perpetuated in its

descendents. The unit on which selection acts (the individual organism) passes unchanged to the next generation. Thus, there is no ambiguity about the unit of selection in this case. However, organisms that reproduce sexually have no alternative but to lose their individual identity when they reproduce. When the genotypes of both progenitors are recombined, the genetic identities are mixed up in the descendents.

Consequently, the offspring are never identical to their parents. In sexual reproduction, gene and organism selections are no longer equivalent. According to gene selectionists, this justifies a change in the unit of selection.

However, the problem is not solved by transferring the unit of selection from organismic level to genetic level. To begin with, as recognized by Williams (1992) himself, genes are not material entities. They are mere packets of information that cannot interact directly with the physical world. The distinction between “interactors” and “replicators” (Hull 1989), and between the bodies (on which selective pressures are exercised) and the genes of which they are carriers, is relevant. However, it does not enable us to get around the paradox of sexual reproduction: the lack of correspondence among the supposed objects of selection (the organisms, whose identity is given by a temporary individual genotype) and the identity that is perpetuated in the next generation.

Although sexual reproduction does not preserve the genotype, it does conserve the genome, which is the set of genes that defines each species. The transience of individual genotypes does not prevent our offspring from being human like ourselves, rather than, say, chimpanzees or lizards. The identity of the species is perpetuated in the next generation.

What has confused theoretical neo-Darwinists is the fact that, from the perspective of the individual progenitor, sexual reproduction does not seem to have an unequivocal selective value to compensate for the presumed immediate benefits of the asexual option. However, as suggested by August Weismann over a century ago, sex does not directly increase the average aptitude but the variance in aptitude. As a result, it also increases the response to selection (Weismann 1889, 1904). In other words, individuals that reproduce sexually have more variable progenies, which ensures that their descendents can adapt more rapidly. However, in the sexual case, what is selected is not a clone with optimum aptitude but a clade (that is, a set of organisms that are related through descendency) with a shared gene pool. Hence, the benefits of meiotic sex are found at the levels of clade and gene (both of which are units of selection in the sense proposed by Williams) (Burt 2000).

Thus, if we wish to resolve the paradox of sex, then we must restore the correspondence between individuality as the object of selection and selected identity. This can be achieved by rising above the organismic level, rather than by dropping down to the level of genes. We must define a higher-level individuality so that the selected genes define the collective identity

that is perpetuated in the next generation (García Leal 2006, 2008).

Therefore, what is the relevant individuality for selection purposes in sexual reproduction? It is no longer the male or the female separately, but the minimal group made up of the pair of progenitors. The genetic continuity of both members is dependent on their reproductive success as a whole. The identity that is perpetuated is not the genotype, but rather that defined by a reproductively compatible genome and a shared gene pool; in other words, the identity of the species.

The evolutionary invention of meiotic sex involves a new form of independence by association, as the progenitors (who depend on others for reproduction) sacrifice part of their individual independence for greater joint independence. From this perspective, sexual reproduction represents a minimum case of group selection (in this case, a group comprises two individuals: a male and a female), and each reproductive pair represents a higher-level individuality, which is the minimum unit of selection in the sexual case.

### A Darwinian Conception of Individuality

The line of argument in the previous section could be generalized to formulate a definition of biological individuality that is meaningful within the Darwinian conceptual scheme and goes beyond that of individuals in the strictest sense (i.e., organisms).

The general definition that we propose is as follows: *A Darwinian individuality is any living entity that is the object of selection as a whole and has a genetic identity that can be perpetuated.*

Traditionally, the term “individual” was only used for organisms (unicellular or multicellular). However, we consider that the concept of individuality can be extended beyond the logic of all or nothing, by which only organisms are considered to possess individuality. It may be the time to define degrees of individuality, between a minimum (for example a simple, reversible symbiotic association) and a maximum (such as that which we attribute intuitively to organisms). We stress that the degree of individuality that we propose (with shades of grey between black and white) refers to evolutionarily relevant aspects of individuality. This is the exercise that we propose to carry out in the next section.

### Criteria of Individuality

In the literature on the topic, some aspects that characterize biological individuality have been proposed and discussed (see, for example, Buss 1987; Ghiselin 1974, 2009; Hull 1976, 1989; Wilson 1999). We have selected relevant criteria that enable us to minimally quantify the possible degrees of individuality.

What criteria should we apply to higher-level individualities? Two of the principles are explicitly stated in the definition

of Darwinian individuality proposed above: the first is the unit of *selection* and the second is *identity*. A third criterion that is equally fundamental can be found in the definition of biological individuality in the introduction to this article, i.e., *independence*.

In order to refine the evaluation of an eventual degree of individuality, five additional intuitive criteria can be considered: *irreversibility, internal organization, reproduction, development, and compactness*.

Below is our proposal for a scale of individuality. The final score for the living system under consideration depends on the aforementioned eight criteria. If we score each of these components of individuality with one of the three possible states, namely  $-1$ ,  $0$ , or  $1$ , then individuals in the strictest sense (in the usual intuitive meaning of organisms, i.e., compact living systems with a well-defined boundary and highly differentiated parts that are specialized in specific functions) would effortlessly receive the maximum score of 8. Below, we shall examine other examples of living systems with non-null individuality, which are not in the category of individuals but are relevant to Darwinian evolution. To achieve this, we shall consider the eight criteria of individuality separately, and assess each one according to the logic of the concept discussed in each section.

### Unit of Selection

Natural selection acts at various levels of the hierarchy of living matter, including that of genes, the individual organism (the fundamental unit of selection in classical Darwinism), and the species. For it to have evolutionary relevance, a living individuality at any level should constitute a unit of selection. To assess this concept, we can ask ourselves whether the pressure of selection is greater on the whole or on the parts: on the higher-level individuality or on its constituents. We assign  $+1$  if the answer is affirmative,  $-1$  if it is negative, and  $0$  if we consider that there is no significant change in this aspect when we change hierarchical level.

### Identity

To have evolutionary relevance, living individualities must have a genetic identity that can be perpetuated. The highest scores are given for this aspect of individuality when the members of the whole share the same genotype, regardless of the level of organization. This is the case of colonial life forms such as *Volvox* (a hollow sphere of clonal cells) or, at the immediately higher level of organization, corals or siphonophores such as *Physalia*.

When members of the higher-level individuality have been generated sexually, the collective identity is vaguer. This makes it difficult for associations to evolve that are comparable to clonal ones. Kinship increases the genetic identity between the associated members and facilitates things. When this occurs

we can talk of “clan identity.” This is the case of social insects, such as ants and termites (Thorne 1997), and also that of the mole rats, which are the only eusocial mammals that have sterile castes. In this case, genetic uniformity is attained through inbreeding. The genotypic similarity in mole rat colonies of the species *Heterocephalus glaber* has been estimated to be higher than 80% (Reeve et al. 1990). At the limits of this evolutionary tendency to genetic uniformity we should find virtually clonal colonies. This has been confirmed by the recent discovery of fungi-cultivating ants of the genus *Mycocepurus smithii*, which have abandoned sex and now reproduce by parthenogenesis (Himler et al. 2009).

This reflection has a clear impact on the eternal discussion of the levels at which natural selection acts (from the gene to the ecosystem), and provides the concepts required for this discussion. Following is the key question: Does the new individuality have a well-defined identity? We can define collective genetic identity as the intersection between the genotypic identities of the elements that make up the community.

To assess the degree of individuality that a group of individuals has, first we should provide a definition of two magnitudes: the identity of the individuals that form part of the group and the identity of the group in question. We can consider that each individual  $i$  of the  $n$  that form the group is characterized by a collection  $A_i$  of  $\mu_i$  elements,

$$A_i = \{a_i^1, a_i^2, \dots, a_i^{\mu_i}\}, \tag{4}$$

where  $i = 1, 2, \dots, n$  y  $j = 1, \dots, \mu_i$ .

We shall define the collective identity  $\Omega$  of an individuality formed by  $n$  individuals  $A_i$  simply as that of the intersection among all of them:

$$\Omega = \bigcap_{i=1}^n A_i, \tag{5}$$

where  $i = 1, 2, \dots, n$ .

In addition, we shall define the individual identity,  $I_i$ , of the members of the group as the set of elements that are not shared with the other elements of the group:

$$I_i = A_i - \Omega.$$

These definitions are, of course, quite metaphorical and do not correspond necessarily to well-defined genetic elements but are sufficient for our purposes here. The collective identity is minimum (empty) in the case of null intersection ( $\Omega = \phi$ ) and maximum in the case of perfect homogeneity ( $A_i = A = \Omega$ ). In contrast, individual identity is minimum (empty) in the case of perfect homogeneity ( $I_i = \phi$ ) and maximum in the case of null intersection ( $I_i = A$ ). In line with these definitions, it seems sensible to assign the maximum score of +1 to individual associations that are genotypically

identical (i.e., they share the same genotype), 0 to individual associations of the same species (i.e., they share the same genome), and the minimum score of -1 to symbiotic associations between individuals of different species.

### Independence of the Whole From the Parts

An individuality is an independent whole made up of interdependent parts. The most basic mutual dependence is reproductive, for example, between the males and the females of a species that is necessarily sexual, or between the sterile worker castes and the fertile reproductive castes in eusocial insects. The existence of sterile castes does not constitute an evolutionary paradox if the individuality that is the object of selection is transferred to the entire swarm. When this approach is adopted, the fact that workers leave the perpetuation of their genes to a few fertile males and females is not much more paradoxical than the fact that the cells of our bodies leave the perpetuation of their own genes to ovules and spermatozoa produced by our gonads. As William Hamilton demonstrated in the 1960s, the evolution of societies with sterile castes is more feasible the closer the kinship between the sterile and fertile individuals (Hamilton 1964). Note that a clonal colony of ants, as the quoted *Heterocephalus glaber* (Reeve et al. 1990), signifies here a clear increase in the degree of individuality in relation to non-clonal colonies of ants (!)

The interdependence of the members of a higher-level individuality can extend to the provision of food. In colonial siphonophores, such as *Physalia*, some individuals are responsible for capturing food and feeding the colony, whilst others are dedicated to producing gametes.

In contrast, in symbiotic associations, each part usually reproduces independently. The interdependence tends to be related to obtaining nutrients and other resources. One way of consolidating the new collective identity through the subordination of the parts to the whole is by the exchange of genes between symbionts (which Lynn Margulis has called “hypersex”). For example, it is known that many of the genes of the ancestors of mitochondria (cellular organelles whose evolutionary origin can be found in bacterial symbionts) have been incorporated into the chromosomes of the cell nucleus (Margulis 1993; Margulis and Sagan 1997).

Another aspect of the parts sacrificing their independence to the whole is that the individual members of a higher-level individuality are less viable than the whole. The death of an ant is much more likely than the extinction of an ant’s nest. The individuals that make up a higher-level unit of selection can be sacrificed, which explains the evolution of “suicides,” such as soldier ants and termites or bees that die when they sting intruders, in defence of the beehive. The behavior of an ant or a bee cannot be understood in terms of their own survival, but with respect to the survival of the ant’s nest or the beehive.

As before, we can ask ourselves whether the higher-level individuality under consideration is more (+1), equal (0), or less (−1) independent from the uncertainty of the environment than its constituent individuals. In other words, is the whole more (+1), equal (0), or less (−1) viable than the parts? To rephrase again, are the individuals more (+1), equally (0), or less (−1) dedicated to the preservation of the individuality than to the preservation of themselves? This criterion is of great significance, as it is the factor that causes the greatest rise up the hierarchical scale. Individuals group into new individualities as a defence against an environment whose uncertainty is increasing. In a simple herd, individuals are better protected from potential predators than when they are alone. Curiously, the concept of a herd benefits the predator as much as its prey: A particular prey has less probability of being the individual chosen as the victim, and the predator has greater probability of catching prey.

### Irreversibility

The collective identity of an individuality that is constructed by association can be so robust that the new cohesion becomes irreversible. This is the case of multicellularity and, in the immediately higher hierarchical level, colonial siphonophores or eusocial insects. Particularly interesting is the recent discovery of what appears to be the only prokaryotic evolutionary experiment in the path toward an organism that is multicellular in the strict sense, which microbiologists have named *Candidatus Magnetoglobus multicellularis* (Abreu et al. 2007). These are magnetotactic bacteria that are organized into hollow spheres containing between 10 and 40 cells, all of which have as much contact with the external environment as with the internal cavity. This is not the only case of multicellularity in prokaryotes: some bacteria form temporary fruiting bodies and others form filaments. However, the spherical bodies do not have a unicellular stage in their life cycle. Even more interesting in this case is the fact that the multicellularity is completely irreversible: isolated cells cannot survive, even under laboratory conditions (Abreu et al. 2006). With respect to the irreversibility of individuality, *Candidatus Magnetoglobus multicellularis* is certainly a candidate for a high score as an individual.

This case is relevant for two reasons. Firstly, the new multicellular individuality is made up of prokaryotic cells. For this reason alone, the case of *Magnetoglobus* is extremely remarkable. In the framework of a theory of hierarchies, it is an outline of a multicellular organism that has no evolutionary continuity. Secondly, this biological entity would never be classified as an individual within the conceptual scheme that is currently in use. Nevertheless, it seems clear that it is, by far, the set of prokaryotic cells that have gone furthest in their path toward a potential organism. In a yes/no logic (individual or not an individual), this living entity would be considered to have no degree of individuality. Perhaps it merits something

more. This is what we aim to remedy with the conceptual scheme that we propose here.

The question that we should ask here is: to what extent are the individuals that constitute a higher-level individuality capable of disassociating themselves and returning to an independent life? Not at all (+1), to a small extent (0), or to a great extent (−1)? Ants cannot take a step back and return to individual life; neither can the bacteria that make up a *Magnetoglobus* sphere.

### Internal Organization

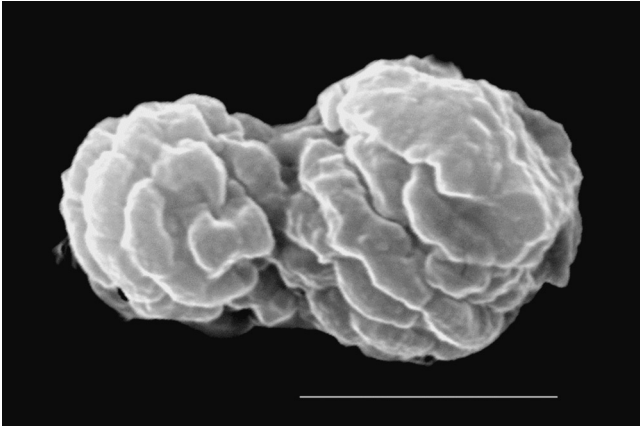
In a higher-level individuality, the functions of the parts are at the service of the whole, which implies that the activities of the associated elements are connected and coordinated. In the case of the aforementioned bacterial spheres, the cells have terminal flagella that enable the whole to move. If each cell were an independent entity, the flagella would move in an uncoordinated way and the sphere would not advance. Each cell has around 20 flagella, which means that there are up to 1,200 per sphere. It is considered that the secret of their synchronization lies in the specialized structures that connect the cells and enable them to intercommunicate. To date, such intercommunication has only been described in eukaryotic organisms (Keim et al. 2004a).

A Darwinian individuality is closer to an individual the more centralized the control of its activities and the functions of its parts. Consider the nucleus of eukaryotic cells or the brains of animals. In this respect, plants are forms of life that are much more decentralized than animals. Thus, animals have a greater degree of individuality. In the case of our bacterial spheres, the cells are simply organized around a central cavity.

Here, the appropriate question is, whether the higher-level individuality exhibits centralization and functional differentiation (+1), some of these characteristics (0), or none of them (−1). For example, there is little more mutual interaction in an aggregate of bacteria than in a simple mass of free bacteria. Internal structure increases when individuals specialize in their tasks to serve the individuality or when a kind of central coordinator of the activities of the individual members appears.

### Reproduction

An individuality (in the sense defined here) begins to seem like an individual (in the classical Darwinian sense) when, in addition to constituting a unit of selection, it represents a reproductive unit, i.e., when the individuality under consideration can give rise to another similar individuality. This is also the case of aforementioned multicellular bacterial spheres. The spheres reproduce as a whole, beginning with the coordinated duplication of the component cells, followed by the division of the whole into two daughter spheres (see Figure 1). The internal cavity does not come into contact with the external cavity at any time during this process and, unlike other prokaryotic



**Figure 1.**

A sphere of *Magnetoglobus multicellularis* dividing itself into two new “individualities.” The white segments means  $5\ \mu\text{m}$  (photo obtained by Henrique Lins and Daniel Acosta-Avalos at the Instituto Militar Engenharia of Rio de Janeiro).

multicellular forms, there is no unicellular state in the biological cycle (Keim et al. 2004b).

Other more complex individualities are the result of a process of development. This is the case of multicellular organisms and, at the immediately higher level of organization, colonial forms such as corals or siphonophores, as well as societies of insects founded by one queen mother.

The question here is, does the individuality reproduce as such? Is it able to engender a new individuality like itself without the need for constituent individuals to reassociate? Does it achieve this completely (+1), partially (0), or not at all (−1)? An isolated worker ant does not reproduce outside the individuality represented by the ant’s nest. In contrast, an ant’s nest engenders another ant’s nest (on the basis of a founding queen, who is to the ant’s nest what the egg is to the multicellular organism). In this section, an ant’s nest will have a better score than any of the worker ants of which it is constituted.

## Development

To what extent do the individuals that make up a supraorganismic individuality have a common history (in terms of growth and differentiation) in the acquisition of their adult steady state? Does the construction of the new individuality occur through a process of growth and differentiation (+1), only growth or differentiation (0), or neither one of the other (−1)? All of the cells in a zebra descend from one zygote. The same cannot be said of the zebras in a herd. An ant descends from an egg, but the entire ant’s nest is not much different, as it descends from one queen who has a quantity of eggs and spermatozoa from the same copulation. The same is true of a termite nest. One of the most spectacular examples of development in a supraorganismic individuality is the sophisticated architecture of *Macrotermes* termite nests and other termites that cultivate fungi. The entire structure is built from an initial

chamber that is excavated by a founding pair. The termite nest then passes through various stages of development until it reaches a mature state, in which it could be more than five meters high and contains up to two million individuals (Grassé and Noirot 1958).

We are aware that this criterion is closely related to the previous one. However, we have decided to separate them because they do not always occur together: a low score could be obtained for reproduction and a higher one for development, and vice versa.

## Compactness

One final criteria of individuality is the existence of an interior and an exterior that are well defined with respect to the group of individuals that constitute the higher-level entity. This is equivalent to stating that, given any point in space, it can be determined whether this point belongs to the interior or exterior of a new collective entity. In mathematical terms, we would say that an entity is geometrically compact when, given two interior points, a line can be found that connects them so that all the points in the path are also interior. A maximally compact organism, such as a bird or *Magnetoglobus*, should be given a score of +1 for this concept. In contrast, an ant’s nest or a herd of zebras, which have minimum compactness, are given the lowest score of −1. Simple aggregates of cells or loosely joined colonies, such as *Volvox*, could be classified with an intermediate score of 0.

Compactness may appear to be an incidental characteristic in the structure of a new individuality. However, we consider that it is relevant for the following reason. A lack of compactness is an insuperable barrier in evolution toward the maximum degree of individuality represented by organisms.

## Conclusions

By way of a preliminary conclusion, we shall apply the conceptual scheme proposed above to seven representative examples, to assess their degree of individuality (Table 1).

As shown in Table 1, the lowest scores were given to the herd and the aggregate of clonal cells. A herd’s only contribution to higher-level individuality is a shared species identity and a slight increase in independence from the uncertainty of the environment (in this case, the sudden attack of a predator). An aggregate of clonal cells shares a genotypic identity and a common origin in a founding cell. Higher, but still low, scores were given to lichen (a representative case of reversible symbiotic association). The comparison between *Magnetoglobus* (a sphere of prokaryotic cells) and *Volvox* (a sphere of eukaryotic cells) is particularly interesting, as a high score is obtained in both the cases (although many biologists would question the individuality of both the groups of cells). The only differences between the two groups are the following. In *Volvox*, there

**Table 1.** Estimation of the degrees of individuality of some relevant living entities following the conceptual scheme developed in this note. These examples are representatives of various groups of organisms (unicellular or multicellular). The herd (a simple coming together of organisms of the same species) represents the minimum level of supraorganismic individuality, a score of -5, while the multicellular organism (which is a group of cells) constitutes a “proper” individual, with a maximum score of 8.

	US	IG	IE	IR	OI	RE	DE	CO	Total
1. Herd	-1	0	1	-1	-1	-1	-1	-1	-5
2. Aggregate of cells	-1	1	0	-1	-1	-1	0	0	-3
3. Lichen	1	-1	1	-1	0	-1	-1	1	-1
4. Ant's nest	1	0	1	1	1	1	1	-1	5
5. <i>Volvox</i>	1	1	1	1	0	1	1	0	6
6. <i>Magnetoglobus</i>	1	1	1	1	0	1	0	1	6
7. <i>Physalia</i>	1	1	1	1	0	1	1	1	7
8. Multicellular organism	1	1	1	1	1	1	1	1	8

Notes: **US** is the unit of selection, **IG** is the genetic identity, **IE** is the independence from the environment, **IR** is irreversibility, **OI** is the internal organization, **RE** is reproduction, **DE** is development, and **CO** is compactness.

is a minimal but fundamental differentiation between somatic cells and reproductive cells (Kirk 1998), while *Magnetoglobus* has a more compact structure. In addition, we should stress the high score of the ant’s nest, which only lacks compactness and a collective genotypic identity (such as that of the aforementioned clonal ants’ nests) to constitute a real superorganism.

One of the pillars of classical Darwinism is being increasingly questioned: the strictly individualist conception of the evolutionary process, according to which the individuals that are the object of selection always act in their own interests. For an increasing number of authors, including even Edward O. Wilson (the father of sociobiology and for some the paradigmatic genetic reductionist), selection on many levels, and not only at the level of selfish genes, should become the theoretical basis of a new type of sociobiology that opposes evolutionary theorists’ rejection of the idea of group selection (e.g., Wilson and Wilson 2007).

We consider that our conceptual scheme, which is based on the notion of Darwinian individuality, enables us to reconcile the defense of group selection with an “individualist” conception of natural selection. In our scheme, group selection is interpreted as the evolutionary emergence of a higher-level individuality.

When uncertainty increases, living systems tend to move up the hierarchical levels of selection by organizing themselves into collective entities that have a greater or lesser degree of individuality. This could be an appropriate conceptual scheme on which to build a theory of hierarchies in the framework of biological evolution.

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## Queries

- AQ1: Author: Please provide E-mail for second author, i.e., Ambrosio García Leal.
- AQ2: Author: Please confirm the change made in edit as "...a whole that is more independent from the uncertainty of the environment than its members individually."
- AQ3: Author: Figure legend is incomplete. Please check.
- AQ4: Author: Please check whether the change made in edit as "score of +1" retains the intended meaning.
- AQ5: Author: Please provide names of all the authors in Reference "Abreu F, Martins JL, et al. (2007)."
- AQ6: Author: Please provide names of all the authors in Reference "Abreu F, Silva KT, et al. (2006)."
- AQ7: Author: Please provide names of all the authors in Reference "Abreu F, Silva KT, et al. (2006)."
- AQ8: Author: Please confirm the changes made in Reference "Himler AG, Caldera EJ, Baer BC, Fernández-Marin H, Mueller UG (2009)."
- AQ9: Author: Please provide names of all the authors in Reference "Keim CN, Abreu F, et al. (2004a)."