

Becoming Organisms: The Organisation of Development and the Development of Organisation

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ABSTRACT - Despite the radical importance of embryology in the development of organismism, developmental biology remains philosophically underexplored as a theoretical and empirical resource to clarify the nature of organisms. This paper discusses how embryology can help develop the organisational definition of the organism as a differentiated, functionally integrated, and autonomous system. I distinguish two conceptions of development in the organisational tradition that yield two different conceptions of the organism: the life-history view claims that organisms can be considered as such during their whole ontogeny; the constitutive view distinguishes two periods in the life history, a period of generation and a period of self-maintenance of a constitutive organisation. Arguing in favour of the constitutive view, it will be claimed that the organisational criteria for the definition of organism (i.e., differentiation, functional integration, and autonomy) can only be applied to the developmental system when it has entered the period of self-maintenance of a constitutive organisation. Under the light of current research in developmental biology, it is possible to make explicit how organisms come to be as organisms. To this end, I explore key ontogenetic events that help us clarify the core aspects of animal organisation and allow us to identify the developmental stage that marks the ontological transition between an organism in potency and an organism in actuality. The structure of this ontogenetic unfolding parallels the conceptual structure of the very notion of organism; the generation of the being of a particular organism parallels its definition.

KEYWORDS – Organicism, development, morphogenesis, functional integration, autonomy

Introduction

The question of what does it mean to be an organism is a longstanding controversy in philosophy of biology and theoretical biology. What “organism” is taken to refer to plays a crucial role in formulating biological theories and different philosophical definitions or conceptualizations of the organism are grounded on different biological disciplines.

Both in theoretical biology and in philosophy of biology, two major traditions can be distinguished as particularly relevant regarding the definition of organism (see also Wilson 2007 and Pradeu 2010, for a philosophical discussion of the contemporary conceptions of the organism). On the one hand, the *Darwinian tradition* is grounded on the theory of natural selection and became the orthodox conception of the organism with the Modern Synthesis. In this framework, organisms are included in the more general category of biological individuals, defined as those entities (not only organisms, but also genes or species) on which natural selection acts. In particular, organisms are conceived as a non-problematic kind of individuals composing populations and their distinct parts are abstracted as adaptive traits that assure their reproductive success within specific environments.¹ On the other hand, the *organisational tradition* considers organisms *per se*, defined as functionally integrated and autonomous systems. Organicism has more ancient and heterogeneous roots than Darwinian evolutionary theory. It traces back to Aristotle and Kant, and during the 19th century it was formulated on the basis of morphology, physiology, developmental biology, and evolutionary theory (see Lenoir 1989 [1982]). During the first half of the 20th century, organicism lived a golden age in developmental biology. The experimental embryology of the late 19th century focused on environmental changes affecting the development of the whole organism, whereas at the turn of the last century, developmental biology focused on the interactions of cells and tissues, incorporating the physiological dimension of development (Gilbert 2004). Between the World Wars, a good part of embryology developed within the framework of organicism showing itself as a middle ground between vitalism and reductionism. Mainly inspired in the regulatory capacities of the embryo, developmental organicism provided the basis of so-called Systems Biology. In the 1960s, the paradigms of genetics overtook those of morphology, physiology, and ethology, and the investigation of the rules underlying the generation of form was abandoned in favour of the study of differential gene expression, behavioural genetics, and sociobiology (Gilbert and Sarkar 2000). However, since the early 1980s, the increasing dissatisfaction with the “received view” (Sterenly and Griffiths 1999) has brought with it new biological disciplines (e. g., in the fields of developmental biology, evo-devo, complex adaptive systems, artificial life, origins of life) and new approaches

¹ Nonetheless, within the Modern Synthesis, different theoretical tendencies must be distinguished regarding the conception of organisms. Some authors such as Mayr or Wright did take into account phenotypic integration, whereas the most “orthodox” version of the synthetic theory – represented by authors such as Fisher, Maynard Smith or Dawkins – have defended an extreme reductionistic view of the organism, conceived as a set of genes codifying adaptive traits.

in theoretical biology and philosophy of biology (e. g., evolutionary systems, biosemiotics, self-organization and complex systems, autopoietic theory) that vindicate the return of organicism (El-Hani and Emmeche 2000; Etxeberria and Umerez 2006). In particular, the questioning of genetic reductionism and adaptationism has led to a revival of organicism in developmental biology and evo-devo (e.g. Gilbert 2000b; Keller 2003; Rieppel 2006; Webster and Goodwin 1996). Thanks to the new experimental and computational tools, biological properties that emerge during development can now be approached and the views of experimental embryologists and system biologists are being recovered (Gilbert and Sarkar 2000, 7).

Hull (1994) has argued that the evolutionary definition of the biological individual as a unit of selection is well grounded on a theory (i.e. the theory of natural selection), whereas the organisational definition is based on phenomenal individuation. Since, according to Hull, there is no physiological or morphological theory, the conception of the organism as a whole composed of functional parts is grounded on our subjective impression and commonsense. However, as the above summary of the history of organicism already suggests, it is far from adequate to claim that there are no available morphological or physiological theories. More importantly, it is misleading to look for *a* theory as *the* unique pillar for a definition of organism. Paraphrasing what Wagner (2000) has argued for evolutionary processes, there are multiple causes and mechanisms involved in the constitution and maintenance of every organism. There is no *single* theory of biological systems but, instead, multiple theories and well-established empirical regularities coming from ecology, ethology, morphology, physiology, biophysics, and genetics that are expected eventually to converge in the explanation of organisms. Developmental biology deals with all these dimensions of living organisation and, as I will try to show, it provides deep insights into the understanding of organisms that have little to do with phenomenal individuation.

What is certainly true is that, despite the historical centrality of embryology in organicism, many contemporary philosophical debates on the definition of organism appear mostly centred on mature states or finished systems, contributing to the adultocentric view that predates biology (Minelli 2003). In the alternative definitions to the Darwinian notion of individuality, development usually appears as a property of organisms (see, e.g. Wilson 2007, section 3) but developing organisms are not explicitly discussed as exemplars of the concept of organism. This particular disregard of development might be attributed to two major forces: (a) the mutual neglect of physiology and developmental biology and, (b) the focus of an important branch of theoretical biology on minimal systems

and the naturalization of biological concepts departing from the physical and chemical study of far-from-equilibrium complex systems.

Regarding the first, the reciprocal divorce between physiology – largely interested in the study of adult organisms (Perlman 2000) – and developmental biology – “chiefly interested in structure rather than function” (Russell 1945, 148) – is an old constant in the history of biology. Although the physiological approach to development was fundamental during the first half of the 20th century, the exclusion of morphology from the Modern Synthesis (Love and Raff 2003) caused developmental biology to turn largely to the neglected problems of form. The dismissal of morphology by genetic reductionism and adaptationism forced the developmental approach of evolution to become focused on the mechanisms of pattern formation that constrain the structure of the morphospace (see, e.g., Alberch 1980).² As a result of this mutual neglect, when philosophy of biology looks into physiology to develop a functional definition of the organism, it turns once again to the adult organism. For instance, Pradeu (2010) bases his definition of organism in the theory of immunology. Although I do agree on the radical importance of the immune system for defining the individuality of the organism, the question of *when* in a life history we can properly talk of “a functionally integrated whole, made up of heterogeneous constituents that are locally interconnected by strong biochemical interactions and controlled by systemic immune interactions that repeat constantly at the same medium intensity” is not faced.

On the other hand, the systemic and biophysical reconstruction of the concept of organism within the fields of the origins of life and minimal forms of life (Gánti 1975; Maturana and Varela 1980; Rosen 1991; Kauffman 1993, chap. 8; see Ruiz-Mirazo et al. 2000 for an overview) overlooked development in characterizing living organisation. Aimed at marking the transition between physico-chemical and biological systems, this research program has focused on cellular or proto-cellular systems (minimal unicellular organisms without development) as paradigmatic models.

As a consequence, developmental biology remains under-explored as a theoretical and empirical resource to clarify the nature of organisms.

² In evolutionary developmental genetics, the term “function” usually refers to molecular functions, such as the function of a protein in the regulation of development, but the “function” I am referring to in this paper is defined at the organismal level. This general distinction being made, it must be added that I do not aim to neglect the importance of functional morphology in evo-devo, nor in the origins of the discipline (Love 2003), nor in the current state of research of developmental evolution (see Laubichler and Maienschein 2009). However, function has been mainly identified with adaptation, and the development of functional organismal integration and of physiological regulation have been poorly studied compared to morphogenesis.

This paper discusses how embryology (including the new fields of behavioural embryology and ecological developmental biology) can help develop the definition of organism as a functionally integrated and autonomous system. To this aim, I first summarize the organisational concept of organism in order to consider whether those approaches oriented towards adult organisms and those referring to developing systems identify organisms as the same entities. I argue that the developing organism does not fully fulfil the requirements of organisational definition at every stage of its ontogeny, because the organism is, in a fundamental sense, an emergent entity. In the light of current research in developmental biology, I make explicit how organisms come to be. To this end, I explore key ontogenetic events that help to clarify core aspects of animal organisation and allow us to identify the developmental stage that marks the transition between an organism in potency and an organism in actuality. As we will see, the structure of this ontogenetic unfolding parallels the conceptual structure of the very notion of organism.

The Organisational Definition of Organism

In the organisational tradition, the concept of organism is grounded in two relational properties: (1) the *whole/parts* relationship, by which an organism is defined as a structural and functionally differentiated and integrated whole and, (2) the *inside/outside* relationship, by which an organism is defined as an autonomous system in relation to its environment.³

Recovering the Kantian discussion of the analogy between organisms and machines (Kant 2001, § 65), we can say that an organism is a *functionally differentiated and integrated whole* in the sense that: (a) like a machine, it is a functional and structural unity composed of differentiated parts playing specific roles within the whole; (b) unlike a machine, an organism cannot be decomposed, because its parts are mutually cause and effect of one another; i.e., their identities depend on their integration in the whole (they can only be understood as emerging from a complex web of integrated processes).⁴ This singularity of biological organisation

³ Both the whole/parts relationship and the inside/outside relationship are intrinsically linked properties, but for the sake of conceptual clarity I present them as two different perspectives on the same phenomenon. Actually, for some authors the term “autonomy” captures both constitutive and relational aspects of living organisation. In this paper I take “autonomy” to refer only to the interactive or system-environment relational aspects of organisms.

⁴ There are two different senses of part-whole relations (Hütteman and Love, under review): a *compositional* relation (that in this case corresponds to structural differentiation and integration) and a *causal* relation (that in this case corresponds to the functional interdependence of organismal parts)

has two main consequences: (1) the constitution and maintenance of an organism does not depend on an external agent, but the organism constructs itself; (2) living parts are not capable of independent existence outside the whole, since their characteristic structural and functional properties depend upon the organic context in which they operate.

Whereas the relationship among organic parts depends on their belonging to the whole, an organism does not stand in an organic relation as part to a wider whole. Instead, it has an environment with which its relations are to a large extent contingent (Woodger 1929, 308). However, the relation of the organism with the environment is, in turn, a constitutive relation, thus having fundamental implications for its definition: (a) the interaction with the environment and the simultaneous definition of the organism's identity are channelled by natural boundaries (cell or skin membranes) which are self-generated by the very system; (b) organisms are able to produce an internally defined identity, what Bernard defined as a *milieu intérieur* or internal environment not governed by the processes of the external environment; and, (c) autonomy does not involve independence because, as a far-from-equilibrium system, the organism is essentially open to exchanges of information, matter, and energy with the environment in order to persevere, but in a manner that is modulated by the organism itself.

The definition of the organism as an integrated whole that interacts in an autonomous way with its environment applies perfectly to both uni- and multi-cellular adult organisms.

. . . cell and skin membranes differentiate internal and external environments; metabolic systems maintain critical physiological parameters for system functioning . . . and, for the more deeply complex multi-cellular organisms, an immune system destroys harmful invaders while a sensori-motor/cognitive system regulates environmental interaction, seeking out critical resources (food, water, shelter, mate) and avoiding danger (poisons, predators etc.). (Christensen and Hooker 2000, 137)

We are prone to think that if a single cell can be identified as an organism, the same will hold for a developing multicellular organism. But can we really apply the organisational definition to all the stages of a life-history? Can the embryo be said to be a differentiated, integrated, and autonomous entity from fertilization – and the subsequent stages of cleavage, gastrulation, germ layer formation, organogenesis, metamorphosis, and adulthood – to death?

In adult organisms, both dimensions of living organisation (functional integration and autonomy) are related to the self-maintenance of the system's organisation, or – to use Spinoza's dictum in the light of Bichat's

reinterpretation – “the endeavour to persevere in its being.” To be sure, self-maintenance does not mean immutable conservation. On the contrary, organisms can regulate themselves in order to adapt to new environmental circumstances. This flexible capacity for re-constitution is the fundamental basis of biological norms “because it marks the emergence of a ‘perspective’ (the continued persistence of the system) against which the outcomes of system processes are measured for success or failure” (Christensen and Hooker 2000).⁵ However, when considering development, Spinoza’s formula falls somehow short as the paradigmatic point of reference to build a theory of organisms. The organised complex of processes that constitute development does not simply restore or adapt normal relations of self-preservation; rather than a self-maintaining entity, the developing system is an ever changing, becoming entity. This apparent “double way of being” of living entities throughout their life-history has yielded two different conceptions of development that – as we will see in the next section – have fundamental consequences for the definition of organism.

The Organisation of Development and the Development of Organisation⁶

The Life History View: The Organism As A Developmental Process

Many developmental biologists claim that the life-history (or even the life cycle) *is* the organism: “The persistence of organization is a primary law of embryonic development” (Lillie 1906, 251; quoted from Ritter 1919, 13). The life-cycle view of the organism was congenial to systems biologists, deeply influenced by Whitehead’s process metaphysics, where natural existence is “understood in terms of processes rather than things – of modes of change rather than fixed stabilities” (Rescher 2008). From this perspective, the anatomist’s timeless concept of the organism is challenged: “the organic form must be comprehended as a cross-section through a spatiotemporal flow of events,” and therefore, what we usually consider an individual is no more than a brief slice of its life cycle (Berta-

⁵In the organisational tradition, both properties ground the teleological and normative dimensions of life in their current organization (Barandiaran and Moreno 2008; Mossio et al. 2009): organisms are *teleological* in the sense that the existence of a process is explained by referring to its effects (i.e. the maintenance of some of the conditions required for its own existence); and organisms are *normative*, since they “must” behave in a certain way in order to exist.

⁶I take the title of this section from a section of the same name belonging to the “Epilegomena” of Needham’s *Chemical Embryology* (1931).

lanffy 1941, 251; quoted from Rieppel 2006). In this view, organisms are defined as spatio-temporal processes or as the sum of their space-time slices. Woodger even claims that organisms do not develop, but they just persist for a time: “it is incorrect to speak of an ovum developing into a frog, it is a temporal part of the history which is the frog ... and the adult is the character of later slices during which changes of a certain type are less rapid and obvious” (Woodger 1929, 294). Thus the very existence of the organism as one thing is seen as depending on the continuation of a type of intrinsic and irreversible change (Woodger 1929, 302-303).

The most radical representative of the process approach was probably Waddington, the founder of “diachronic biology.” In his view, organisms are developmental systems, systems in the process of a becoming that is never achieved. In order to understand the essential dynamic character of organisation, Waddington had to introduce several new terms, such as “canalization,” “creodes,” and “homeorhesis,”⁷ all of them devoted to capture the stability of the whole process of a life history, a pathway of change which is preserved despite of the change of states.

In the life-history view, the meaning of self-maintenance is generalised by making it synonymous with *self-preservation*. Since in the course of its development an organism can exist through a continuous series of different organisational regimes, self-maintenance would thus make reference to the persistence of the system (understood as a dynamic whole) without specifying any particular stable organisational configuration. Many of the mid-20th-century embryologists claimed that wholeness begins with fertilization and continues throughout differentiation. More recently, some theoretical biologists have expressed similar views, defining organisms as “dynamically stable wholes that undergo particular types of transformation” (Webster and Goodwin 1996, 193; see also Rieppel 2006).

The Constitutive View: The Development of Organisation

Aquinas, together with other 13th-century theologians, did not consider abortion to be murder if it occurred before the foetal stage. Human life was thought to start at conception (and therefore, since human beings should not contravene that process, abortion was considered to be a sin). But it was also believed that souls are created individually at

⁷ “Creodes” refer to developmental pathways or trajectories; “canalization” means the ability of developmental pathways to produce normal phenotypes despite perturbations; “homeorhesis” names the resulting stability of the developmental process (see, e.g. Waddington 1957, and Gilbert 2000b for a review of Waddington’s concepts).

each generation (and therefore no actual murder of a proper human individual could take place before the foetal stage; Regan 2003, xxv). As it is well known, Aquinas's position was deeply influenced by Aristotle's conception of the soul, defined as "the first grade of actuality of a natural body having life potentially in it" (*De anima*, II 1).⁸ In the *Generation of Animals*, Aristotle claimed that since conception, the organism is an organism in potency. The potency of becoming an individual of a certain species is progressively actualised by the differentiating movements that sperm unleashes on the maternal matter, but the organism is not ensouled and thus it is not an organism in actuality until it is fully morphologically differentiated and functionally active. Since Aristotle, teleologists have claimed that developmental processes cannot be understood without appealing to "their relation to the biological end of self-completion" (Russell 1945, 93) or self-realization. The teleological view of ontogenesis has been driven by the ascertainment of the "equifinality" of development (Driesch 1908): developing organisms, departing from different initial conditions or going through different pathways, can reach the same endpoint. Since the late-19th century, the regulatory capacities of embryos have been widely explored by experimental embryology, showing that both the development of the whole organism and the morphogenesis of particular organs are highly resistant to perturbations. Later on, this robustness of development was seen to be typical of self-organized systems standing at the edge of chaos, in far-from-equilibrium conditions and remaining both stable to perturbations yet sensitive to internal fluctuations and environmental variations that can be selectively amplified by the system to reach other meta-stable states (Kauffman 1993). Within the framework of dynamical systems theory, ontogenetic stages can be modelled as the temporally stable attractor states of the developing embryo and the finished organism as the final equilibrium state of the system. An example of this approach is René Thom's "dynamic structuralism." Inspired by Aristotle, D'Arcy Thompson, and Waddington, Thom considers development as a process of continuous dynamical "fight" among "fields" or "archetypes" which generates a "geometrically stable configuration" (Thom 1968, 166).

From this point of view, Spinoza's formula is interpreted in Aristotelian terms as the endeavour to bring the essence of an organic being into

⁸ In fact, the Aristotelian distinction between potency and actuality continues to play a key role in the contemporary debates on human cloning and abortion. A recent Report of the United States' President's Council on Bioethics (2002) on the issue of cloning for biomedical research gives a good account of the different positions being held on this respect. Leaving aside the ethical, moral, and political reasons, the ontological arguments regarding the problem on when a human embryo can be considered a human being can be extended to all animals.

completeness, a movement from potentiality to the actualisation of all that any creature is capable of becoming (Russell 1945, 191). Self-maintenance is seen as the main purpose of the adult organism, and the movement towards self-maintenance, or becoming a self-maintaining organization as the main goal of the developing organism. In fact, most of the organisational definitions consider development as a different goal from that of self-maintenance. For instance, Bertalanffy defines the organism as a system that “is generated *or* remains in the state characteristic of it” (1933, 49; *my emphasis*).

How and When Organisms Come To Be

Some extreme views of genetic determinism entail a conception of the organism as an epiphenomenon of its genes, a mosaic of discrete entities directly mapped into discrete phenotypic traits. From this point of view, the essence of the organism is identified with its genotype and hence development poses no challenge to the organism’s definition. In the context of the debate on cloning, genetic identity has been used to hold that the embryo’s human and individual identity is present from the start (President’s Council on Bioethics 2002, 154). However, in the developmental organisational tradition (both in the life history and in the constitutive view) “development is not seen as an unfolding of something preexistent, but as a coming into being” (Maienschein 2007, 112). Therefore, embryology is conceived as the study of epigenetic emergence, as opposed to preformationism (Maienschein 2007, 112). One of the main principles of organicism is precisely that the properties at one level of complexity (e.g., cells or tissues) cannot be ascribed directly to their component parts (e.g., genes), because they *arise* through the interactions among the parts. Thus, in this view, different laws or rules are appropriate for each level of the irreducible hierarchy of living organisation (Gilbert and Sarkar 2000). Developmental processes – even at the genotypic scale – proceed through interactions at different levels of organization (Hall 2003; see Salazar-Ciudad et al. 2003 for a classification of the developmental mechanisms responsible for pattern formation).

At every level of organisation, development is highly organised and ontogenetic rules are context-dependent. In this sense, “the organism is ontologically prior to any of its functional structures, such as adaptations, life history traits, or developmental systems” (Laubichler and Wagner 2000, 293). Therefore, in a sense, the life history (or even the life cycle) *is* the organism (Gilbert 2000a). But if we take seriously the fact that the hierarchy of multicellular organisation is created during development,

we cannot properly say that an organism self-generates or that, during a certain period of its life, the organism has the goal of self-generation. What we can say is that at the beginning of a life history, there is a self-generating system that *in potentia* is an organism of a particular species. As Needham warned, “heredity does not account for the individual but for a number of potentialities, some of which are brought into being in the individual” (Needham 1931, 567). Hence, the transition of the gamete-cells merging into a zygote cannot be considered the same as that in which this new entity becomes the multicellular individual organism, precisely because living organisation is an emergent order. I thus claim that it is essential to recover the classical distinction between an organism in potency and an organism in actuality and, on the basis of current embryological knowledge, to formulate a constitutive definition of organism. But when can we consider that an organism is in actuality?

Commonsense identifies the organism in actuality with the organism that lives in the external environment after birth or hatching. This is a widely implicit assumption in ethology and developmental psychology: embryogenesis is identified with innateness and the organism’s autonomy is thought to start when it comes into the world.

However, birth and hatching are arbitrary time-markers for the beginning of the organism, mainly for two reasons (Michel and Moore 1995, 290). First, birth and hatching occur at different developmental stages in different species; most animals go through a larval stage that is radically different from the adult stage. Even confining ourselves to those species with direct development, some of them (fishes and reptiles) are born as miniature adults, whereas others (birds and mammals) undergo a period of neonatal immaturity. Actually, all of them can hatch or be born earlier than usual and still be viable organisms. Second, life in the embryological environment and life after birth or hatching are more continuous than it might appear. Of course, life confined within an egg or an uterus and the outside life involves important differences in neural organization, sensory-motor capacities, physiological requirements, and environmental context. However, differences between both environments, such as the amount of space available for movement, may be responsible for behavioural differences, producing the impression that embryos and neonates are more different than they actually are. Thus, embryonic behaviour cannot be thought just as a functionless epiphenomenon or as a preparation for adult behaviour, but as an ontogenetic adaptation (see a review in Oppenheim 2001). Teratologies offer a good illustration of this fact. Development often leads to functionally integrated and viable monsters.⁹

⁹Development does not always lead to the adult organisation typical for the species; it sometimes gives rise to *the monsters typical for the species*. The alternative to normal development is far from be-

Defects in the lungs, limbs, face, or mouth, are not deleterious to the foetus (which does not depend on those organs while inside the embryological niche), but can threaten life once the organism is born (Gilbert 2000a, chap. 21). Therefore, the goals of development (understood as the possible metastable end-states or forms of organization that developmental processes can generate) cannot be identified with the goal of self-maintenance outside the embryological niche because what can persist in the embryological environment is not identical to what can persist in the external world.

In the following, I will analyse the main developmental stages of developing animals in order to check whether the characteristic properties that the organisational tradition attributes to organisms can be applied to each of them. In order to do so (as Schmalhausen proposed), development will be analysed as a morphophysiological process, taking into account how different forms of interactions play different roles and dominate different stages of ontogeny¹⁰ (see Table 1 for a summary).

ONTOGENETIC STAGE	ORGANISATIONAL INTEGRATION		AUTONOMY		
	<i>Differentiated parts</i>	<i>Global interactions</i>	<i>Internal environment</i>	<i>Boundary</i>	<i>System-environment coupling</i>
<i>Oogenesis-zigote stage</i>	Intracellular parts (molecules, macromolecules, organelles)	No	Yes	Yes	No
<i>Cleavage</i>	Cells	No	No	No	No
<i>Gastrulation</i>	Germ layers	No	No	No	Partial
<i>Organogenesis</i>	Morphogenetic fields	No	Partial	Partial	Partial
<i>End of organogenesis</i>	Organs	Yes	Yes	Yes	Yes

Table 1. Summary of the fulfilment of the organisational criteria in animal development (see text for details).

In my analysis of the diachronic transformation of organization, I shall confine myself to animal development and, particularly, to vertebrate development. For of course, I do not intend to use vertebrate development as a model for the definition of every kingdom, nor for every animal phylum. The embryological specification of the necessary criteria to identify an organism will vary depending on the species; a search for the actuality of the vertebrate organism will yield a definition of the vertebrate organism. My aim here is to depart from well-known embryological examples in order to illustrate how the organism's constitutive properties (func-

ing a random variation within the phenotypic space; rather, there is an underlying "logic of monsters" that cannot be explained by blind variation and natural selection, but reveals the logic or the organisation of development (Alberch 1989; see Etxeberria and Nuño de la Rosa 2009).

¹⁰ See Levit et al. (2006) for a review of Schmalhausen's theoretical biology.

tional integrity and autonomy) become progressively actualised during development, showing that what is true for a cell might be paradoxically untrue for a multicellular nascent organism.

The Development of Organisational Differentiation and Integration

Since von Baer established it as the fundamental law of ontogeny, many developmental biologists have emphasized that “the developmental history of the individual is the history of the growing individuality in every respect” (von Baer 1828, 263; quoted from Russell 1916, 178). Ritter dedicated an entire book to study what he called *bio-integration*, “the process of moving on from grade to grade of interdependence among the differentiating parts” (1919, 94), and Woodger (1929) characterised development as a gradual rise in the level of organisation of the embryo. While acknowledging this fundamental fact, I contend that this process of integration reaches an ontological threshold where it can be said that the organism has come into being.

From oogenesis to the zygote stage

Developmental biologists consider that development does not properly start at fertilisation but at oogenesis. Both before and immediately after fertilization, the multicellular organism is in fact unicellular, governed by interactions between pre-existing genetic products. We can claim that during this period, the *zygote* fulfils the requirements that the organisational definition has applied to unicellular life (e.g., Christensen and Hooker 2000). Like in a bacterium, the zygote’s differentiated parts are bound by globally organised interactions and, in this sense, it satisfies the condition of functional integration. Indeed this holistic organisation explains that (like in unicellular organisms) cutting a zygote in two does not produce two new zygotes.

Cleavage

The first stage of organisation lasts for a very short time. During cleavage, the zygote is divided into smaller cells (blastomeres) that at the end of this stage form a blastula, a spherical (and almost uniform) ball of cells. After the first cell division, the developing organism becomes a multicellular organism, entering a new type of organisation where it is no longer the whole, but the parts that are characterized by the cell-type organisation (Woodger 1929, 296).

At the cleavage stage, the holistic organisation of the dividing embryo is difficult to assess. The classical Driesch and Spemann experiments on

the partition of blastulas illustrate this difficulty. Driesch showed that if the cells of a sea-urchin's blastula were separated at the early stages of cleavage, two complete embryos were obtained. Spemann repeated the experiment with salamander's eggs, but instead of completely separating the blastomeres, he tied a fine hair to isolate the cells. When the constriction crossed the median plane of the embryo, bisecting the blastopore, two complete embryos were obtained, like in Driesch's experiments. However, if the constriction was made so that only one cell contained the blastopore, the cell developed into a complete new whole, while the other formed an undifferentiated belly mass that eventually died. Spemann's experiments showed that the cleavage furrow established the dorso-ventral axis of the future body organization and that the future blastopore region of the egg was essential for differentiation.

The results of Driesch and Spemann set a paradox for the definition of the organism as a functional whole. On the one hand, "they emphasized the holistic nature of development as a process not limited to changes in individual cells, but a property of the entire organism" (Allen 2006, 141). However, from the point of view of the current organisation, Driesch's and Spemann's results also showed that the properties of a blastomere remain the same regardless of being in its place in the organic whole or being removed from it. This dual nature of the blastula (i.e., its regulative capacities and its mosaic character) allowed it to be used as an illustration of the different metaphorical models of the part-whole relation which – according to Canguilhem – permeate the history of biology (Gayon 1998). One such model is the *political model*, which considers parts as individuals, like citizens in the Republic. This metaphor underlies several mosaic theories of development (Roux, Wilson) that conceived of the (multicellular) organism as a symbiosis of independent (unicellular) organisms. On the contrary, according to the advocates of the primacy of organismic unity (Ritter, Huxley, Whitman, Child), the *technological model* accounted better for the understanding of embryogenesis. From the beginning of development, organic parts (cells in particular) are analogous to differentiated tools that converge into the maintenance of the organismal whole.

Both models capture portions of the truth. Early cleavage is mainly determined by molecular and physical mechanisms at the level of the individual cell, where cell-cell interactions play no role. Only at a later stage will morphogenesis be directed by the positional specification and cytodifferentiation of cells. The role of mechanical and signalling interactions in cleavage is currently under study and it has been demonstrated that even in mosaic development (where cell specification is determined at the cleavage stage) the fate of most of the cells depends

on appropriate cell interactions (Gardner and Stern 1993). Nonetheless, there is a general agreement that such interactions are local in nature. The absence of functional interactions among parts in the early blastula explains precisely the phenomenon of totipotency characteristic of deuterostome cleavage (i.e. the capacity of the parts to become a full organism when separated). It thus might be said that, at the cleavage stage, the developing organism is better understood under the light of the political model, whereas when looking at its future stage, the becoming organism is better understood by means of the technological analogy.

Gastrulation

The developmental stage following cleavage is gastrulation. In the course of this period, coordinated cell movements lead to a massive re-organization of the blastula into a trilaminar structure (the ectoderm, the endoderm, and the mesoderm).

From the onset of gastrulation, cells irreversibly lose their capacity of self-differentiating into new organismal wholes. Taking into account the impossibility of twinning at this stage, some bioethicists have opposed the cloning of human embryos beyond the blastocyst stage (The President's Council on Bioethics 2002, position 1 and 2; Alvargonzález 2009). Taking the word individual in its etymological sense (an individual is an indivisible entity), it is denied that before the onset of gastrulation there is an individual, since it is unclear whether it will develop into one or more human beings. After the primitive streak is formed, the embryo cannot divide itself or be divided to form another being and thus it can no longer be anything but a single entity. However, according to the organisational tradition, individual determination is not a sufficient condition for the definition of organism. The reason is that individuality and functional integration are not only *conceptually* separable properties, developmental biology shows that they are also *temporally* dissociated processes. The irreversible loss of totipotency does not coincide with the achievement of functional differentiation and integrity. After the establishment of the three germ layers, the interactions that characterize development occur among groups of similar cells within the germ layers, but there are few inductive events.¹¹ Therefore, at the gastrula stage we have a system with structurally and functionally differentiated parts (i.e. the germ layers) that is nevertheless not integrated by global interactions. Actually, if a gastrula is cut into two, each half develops more

¹¹*Induction* is the process by which a group of cells changes the behaviour of an adjacent group of cells, causing a change in their form, mitotic rate, or fate.

or less independently of the other, forming only those organs which it would have formed as part of the whole.

Organogenesis

Once the three germ layers are established, they interact and rearrange themselves to produce tissues, whose interactions produce organs. In the case of vertebrates, within the period of organogenesis it is necessary to distinguish two important events for the definition of organism. During neurulation, many global inductive events occur simultaneously, and the modules overlap and interact with one another. For instance, failure to induce the mesoderm in a certain region, leads to malformations of the kidneys, limbs, and tail. At the neurula stage we can thus talk of a true organismal integrity. However, after the major body plan is fixed, most of the inductive events occur again within discrete modules and organs develop in a semi-autonomous fashion from distinct clusters of cells (Raff 1996; Wagner 1996). Incipient organs are morphogenetic fields (Gilbert et al. 1996); they can be cut and pasted into different locations of the embryo, they can be cut into two, they can accommodate alien cells (including other species' tissues as in the case of chimeras) and, yet, they develop normally into complete organs. Tissues and organs have, so to speak, an independent life, and the embryo at this stage is a kind of composite organism. This explains why if the induction of a particular organ fails only this organ is affected; an accurate coordination in tissue and organ morphogenesis is not essential for the production of viable offspring (Gardner and Stern 1993). Nevertheless, we face a crucial moment in the constitution of living organisation, because the specialised parts that will be further integrated are being defined; i.e., organismal parts are individuated in development (Wagner 1989).

The regulatory capacities of morphogenetic fields are progressively lost throughout development, until re-differentiation is no longer possible. This moment coincides precisely with the onset of function, since (as well as form) the capacity of the biological system to carry out operations can be defined at different levels of organisation (Waddington et al. 2009). At the end of organogenesis, the extensive elaboration and integration of the embryo's anatomical and physiological systems takes place. At the same time, once organogenesis is completed, further differentiation as well as the maintenance of what is already formed may be dependent on functional activity. There are many examples of this phenomenon of nesting of development and function (Michel and Moore 1995, 298-299; Needham 1931). One such example is the development of the circulatory system, in which the structure and constitution of

blood-vessels depend on their use by the circulation as a whole. Other examples include the co-development of limbs and certain parts of the nervous system (whereby spontaneous muscle activity guides the growth and migration of nerves and neurally induced movements guide the formation of cartilages), the correlation between diet and the development of the intestine, etc. Both functional integration and the emergence of organismal function (contributing to self-maintenance and self-generation) are crucial events for coming-into-being as an organism.

The Development of Autonomy

Like functional integration, autonomy is difficult to grasp in the early developing embryo. We should remember that, in the current account, autonomy implies (a) an internal environment (b) a self-created boundary and, (c) an internally guided regulation of the system-environment coupling. I shall argue that all of these dimensions of autonomy do not just differ in degree in the developing embryo and in the organism in actuality, but they are achieved in the course of development.

Like organismal integration, the existence of an internal environment is an intermittent characteristic of the developing organism:

[T]he germ cells that unite to form the fertilized egg do have in a certain sense an internal environment inside the body of the parent organism. When they are cast loose they cease for a time to have such an environment, and it is only after cleavage begins that the resulting cells acquire a new internal environment in their sister cells. For a short period this is the only internal factor that counts, there being as yet no general milieu intérieur [...] Later, after the establishment of a circulating medium and the primitive nerve paths, an internal environment of the ordinary sort is again present. (Harrison 1940)

The possession of a self-created boundary is also a late event. Until the closure of the body wall, the embryo does not have a proper boundary that distinguishes itself from the environment while serving to regulate the system-environment relationships. Before folding, the embryo is, as a matter of fact, a trilaminar germ disc. Only after suffering four body folds – i.e., the cephalic fold (head), the two lateral folds (sides), and the caudal fold (tail) – it acquires a three-dimensional structure. The body wall is progressively established but lateral body walls do not meet and fuse at the ventral midline of the embryo until the end of organogenesis (Brewer and Williams 2004). Only from that crucial moment on, the organism possesses not only a skin, but also a functional immune system and a nervous system through which it interacts with the external envi-

ronment that becomes an increasingly important contextual element for the whole developmental system (Michel and Moore 1995, 285).

Regarding the system-environment coupling, the relationship of the embryo with the environment is also radically different when the organism is in potency and when it is in actuality. From this view, the first remarkable fact is that developing organisms have two environments: the embryological and the outside environment.

The external environment can be described as belonging to developing organisms, since it controls or fixes crucial developmental parameters. As ecological developmental biology has shown, environmental interactions with developmental processes are not only essential, but they can be responsible for fundamental adaptations. The environment may induce several organismal changes: specific adaptations according to the season, morphological changes that allow to escape predation, caste determination in insects, sexual phenotype determination, alteration of neural structure, specification of immunocompetent cells, etc. (Gilbert 2004; for a detailed analysis of ecological developmental biology see Gilbert and Epel 2008).

On the other hand, development is achieved in an extremely stable embryological environment. As a matter of fact, this is the only niche where a living part is capable of independent existence: a gamete (as a part of the progenitor) and a blastomere (as a part of the embryo) are only capable of becoming new wholes within completely organic environments. During development, the organism is more an extended phenotype than it will ever be in any other period of its life. Christensen and Hooker (2000) refer to the organisation of interactions that allow organisms to acquire resources and direct them into the re-constitution of themselves as the system's "directive organisation." Directive organisation admits a wide spectrum of completion: the more autonomous the organism, the higher its directed organisation. Those systems (like viruses) that rely essentially on external sources of organisation (i.e., on other systems, such as the machinery of a host cell) to structure the processes necessary for their cohesion, present an "incomplete directed organisation." What is not usually considered is that the most extreme case of incomplete directed organization (setting aside parasites) is found in the most complex developing organisms. Development of multicellular organisms is, in fact, a co-development. Probably the most perplexing example of the dependency on the mother of a crucial aspect on ontogenesis is given by the specification of body axes in *Drosophila*. Specification of the anterior-posterior axis involves three largely independent systems. All of them depend crucially on the activity of the maternal genome either in the oocyte or in its associated

nurse or follicular cells (see Gardner and Stern 1993 for references) that induce the establishment of the anterior-posterior axis.

Indeed, it appears to be an empirical principle that the more autonomous the adult organism, the longer the period of incomplete autonomy it goes through during its development. The most extreme case is given by mammal's development, whose progressive achievement of autonomy can be summarized as follows (Gilbert 2000a, chap. 11). At the morula stage, the embryo consists of a small group of internal cells surrounded by external cells. The embryo (and its associated yolk sac, allantois, and amnion) is derived from the inner cells, whereas most of the descendants of the external cells become the trophoblast cells, which fuse with the uterine wall and produce the embryonic portion of the placenta. The distinction between trophoblast and inner cells is the first differentiation event in mammalian development and it is required to adhere to the uterus. Once attached, the chorion enables the foetus to get oxygen and nutrients from the mother and the foetus sends its waste products into the maternal circulation, while constantly producing hormones and regulators of the immune response in order to avoid the rejection of the mother. Therefore, before implantation, the embryo is not recognized by the mother as an independent organism. Only when it adheres to the uterus it might be said that the embryo has some sense of a self that distinguishes itself from the environment it inhabits, having needs which are distinct from the needs of the organism that hosts it. This is a crucial event, since the organism self-defines as a different entity (to the extent that it has to actively inhibit the mother's tendency to reject it as an alien system).

Again, we cannot speak of a complete autonomy at the foetal stage. Mammalian foetuses lack functional lungs and intestines, and, as we saw, oxygen and nutrients must come from the maternal blood. As a matter of fact, in many cases complete autonomy is not achieved even once organisms are born. Those species that undergo postnatal immaturity strongly depend on parental care until much later stages. However, as soon as the nervous system interacts with the rest of the body (integrating and regulating function) and as the organism begins to interact with its environment in a directed and integrated manner we can start talking of a progressively autonomous yet *complete organism*. This is precisely the research focus of behavioural embryology (Michel and Moore 1995), which has demonstrated that many aspects of nervous system and behavioural development (including learning) have their origin in embryological behavioural and experiential events. The holistic quality of behaviour is due to the appearance of experience, broadly defined as "the contribution of

functional activity at the behavioural and neural levels of analysis, whether the activity arises from external or internal sources” (Gottlieb 2001).

Self-generated experience and stimulation from the external world affect the developing nervous system through processes that are continuous at the cellular and regional levels with those that were described for neuroembryology. Although the processes do not differ when considered at the level of neurons and their interconnections, the addition of sensory inputs from external and self-generated sources provides a new element to the system. This creates a new level of organization. At this new level, contextual effects continue to be important, but are best described in terms of the interaction between the organism and its environment, and the organism’s environment is predominantly a sensory one . . . (Michel and Moore 1995, 284)

In summary, before the end of organogenesis, the embryo goes through alternative periods of holistic and mosaic development, autonomy without individuality, individuality without autonomy, extreme sensitivity to perturbations and strong robustness and, at the same time, it loses and acquires an internal environment. Sometimes these events overlap, sometimes they happen at well differentiated stages. *Development is a highly organized process, but it only achieves a stable morpho-physiological order when organisational integration and autonomy converge at a true organismal scale.*

The Organism in Actuality

The current state of embryological knowledge allows us to acquire a deeper meaning of Aristotle’s conception of the process of coming-into-being. Before the completion of organogenesis, an organism can be said to exist in potency. As we have seen, the individual organism is progressively actualised. At the beginning, every cell is, in potency, an organism; later on every cell is, in potency, a part of a part whatsoever. Finally, each part is in actuality what it is. Once organogenesis is completed and endowed with nervous and hormone control, organs are in a usable stage and therefore they appear in a state of first actuality; i.e., they have the capacity to function as integrated parts of an organismal system. At the larval or foetus stage, most sensory systems are functional (Gottlieb 1971) and the whole organism engages in an activity that for the first time involves coordination among its specialised parts. There is here an emergence of a new and fundamental mode of organisation. After this happens, “a shift has taken place in the level that requires explanation, and a new set of terms

and explanatory principles becomes necessary” (Michel and Moore 1995, 284).¹²

The radical ontological importance of this developmental event has indeed been captured by embryology in two classical distinctions of developmental periods. From a morphological perspective, two periods are often distinguished in development: a period of “qualitative” development, which involves an alteration in the nature of the system and a period of “quantitative” development, where change consists of a quantitative change in a system (growth) that remains essentially unaltered (Waddington et al. 2009).¹³ From a physiological perspective, Roux, and later on other developmental biologists such as Woodger, Russell, or Needham, distinguished two main (partly overlapping) periods in the ontogeny of Metazoa: an automatic period of self-differentiation, covering from fertilization to the end of organogenesis, throughout which the separate parts of the embryo show functional independence of one another; and a functional period devoted to the functional integration of all organs within the whole.

The morphological distinction and the physiological distinction are coincident. While it is usual to read that the notion of foetus is no more than a conventional landmark (see, e.g. Biggers 1990), the foetus stage (or the larval stage in those species undergoing metamorphosis, such as the tadpole stage in frogs) is not an arbitrary category. The difficulty of neatly demarcating the precise transition between an organism in potency and in actuality must be acknowledged, but this is a challenge faced by the attempts to mark out almost any transition in the biological domain. In particular, the life-history view also includes a fuzzy delimitation of the birth of an organism. As we saw, life-history is usually claimed to start not at fertilization but at oogenesis, which easily transforms the life-history into the life-cycle.

At the foetus or larval stage, the organism is morphologically and functionally mature and therefore, form and function can be strictly defined for the first time at the organismal level. Structure encompasses all parts of the organism capable of carrying out functions. In other words, a non-reducible kind of compositional relation (i.e. that between organismal wholes and in-

¹² Although Michel and Moore are talking of the biological grounds of the discipline of behavioural embryology, my claim is that the same ontological shift marks the existence of the organism as such and that, as a consequence, the definition of organism has to consider this fundamental fact.

¹³ To be sure, pure quantitative development is never found: the developmental period up to adulthood involves not only growth but also processes of maturation that include qualitative changes. Nevertheless, there is no doubt that when an animal has attained a structure with the full complement of organs, it enters a period of mainly simple growth, where it increases not in complexity but in size, i.e., quantitatively.

dividualised organismal parts) is needed for the emergence of an also higher level causal whole/parts relationship (functional integration). Only then may an organism be properly said to be a functionally integrated and autonomous system. From then onwards, the maintenance of structuro-functional integrity or wholeness becomes a fundamental condition of active life, in such degree that the activities essential to life must be carried on in a coordinated and integrated manner (Russell 1945, 11). Thus, the developing system becomes an *organism*.

Conclusion

As it has been shown for other biological concepts, such as the concept of homology (Brigandt 2003), the concept of organism plays different theoretical roles depending on the epistemic goals of different research approaches, that will thus yield different definitions of organisms.¹⁴ As discussed throughout this paper, the life-history and the constitutive views do not identify the organism as the same entity. The whole life history can be considered as the organism in the sense that a living entity remains the same notwithstanding the possible transformations it could incur throughout its life-time. However, an organism is much more than an entity persisting in time, and the main criteria of the organisational definition are far from satisfied at each stage of ontogeny. Functional integration and the achievement of autonomy are late events in development. Therefore, from the point of view of current organisation, we cannot properly talk of an organism in actuality until it has entered the quantitative and functional period. A constitutive definition of the organism is needed.

Embryology illustrates and completes the more abstract definitions of organism developed within the realm of minimal unicellular systems. As Aristotle thought, the essence (and, at the conceptual level, the definition) of a being (or its concept) cannot be understood unless we understand its *ontogenesis*; that is to say, the generation of the being of a particular organism parallels its definition. The developmental process

¹⁴ According to the reformulation of the criterion of *biological genidentity* developed by Boniolo and Carrara (2004), a biological entity can be abstractly defined as a non-additive complex of three kinds of properties: those concerning its space-temporal position; those concerning its being a living entity; and those which are interesting from a particular biological point of view. Thus what is defined as a living entity persisting in time, depends on the biological approach. This is precisely what happens in the definitions of organism. As I have argued, the emergence of new and irreducible modes of organisation makes necessary the introduction of a new biological view that identifies organisms as different biological entities.

of a living system conceptually recapitulates the definitional criteria for the organism. We can thus offer the kind of definition recommended by Aristotle in his *Metaphysics*: that where the parts of the definition are the same parts of the described entity and the concept of the living thing is, in the end, the living thing itself.

If developmental biology must be considered as a fundamental discipline for philosophical and scientific-theoretical conception of organisms it is not only because it explains how organisms come to be, but because organisms come to be in development. Development is not only a creative period of self-generation, in contrast to the reductionist view of development as the unfolding of a genetic program. It is also (continuing from the moment when an organism is in actuality) a fundamental period of the organism's life. It is in the embryological environment that the organism has, for the first time, a meaningful environment and this has fundamental consequences for the understanding of the nature and behaviour of the organism.

Needless to say, the present analysis of the developing organism is a preliminary one and further philosophical research remains still ahead. For instance, each of the developmental stages should be analysed much more carefully, regarding the whole integrity and the autonomy of the developing organism. On the other hand, most of the argument presented here has focused on vertebrate development. In other kingdoms and other animal phyla, different actuality points (i.e., different embryological events happening in different ontogenetic stages) than those identified in this paper can be found. Besides, the species discussed here undergo progressive and single-phase development, where morphogenesis leads to increases in size and complexity that persist throughout the whole life. Therefore, I have not faced the challenges posed by metamorphosis and regressive development. Metamorphosis is a challenging question especially in those cases where the alteration between the larval and the adult forms is drastic. For instance, during sea urchin metamorphosis nearly all the structures of the larva disappear and the five-rayed adult develops from a very small rudiment within the larva. Regressive development is even more challenging: certain species (like barnacles) at an early stage develop a relatively complex structure that enable them to be motile, and they later adopt a stationary form for which motility is no longer necessary. My view is that in both cases we can speak of an organism as encompassing two types of living organisation. But these are matters for another paper; for the time being the present contribution shall get to an end where the organism starts, autonomously dealing with its own environment while seeking to persist as an integrated whole.

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